

Lillie Browne 28.



Chickadee

1. fish

2. birds

3. salamander

4. anthropoids

5. spider

bee

Lillie Browne '28,
776 North 2nd West,

THE ANIMAL MIND



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THE ANIMAL BEHAVIOR SERIES

THE ANIMAL MIND

A Text-Book of Comparative Psychology

BY

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THIRD EDITION

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PREFACE TO THE THIRD EDITION

Again the accumulation of material during a nine-year period has made necessary the rewriting of a large portion of this book. Particularly noteworthy in the last five years have been the German contributions, especially those thorough experimental studies of sensory discrimination published in the new *Zeitschrift für vergleichende Physiologie*. The work of the Amsterdam laboratory of physiology is also a welcome addition to our resources. In the present edition of "The Animal Mind," the chapters dealing with sensory discriminations and with the tropism, besides incorporating the new material, have been thoroughly reorganized so as to give, it is hoped, a much clearer survey of the complex mass of data they present, and thus to make them more readable. The treatment of perception has been considerably changed, and takes account of the work of the configurationists in the field of animal psychology. The treatment of learning enters more fully into theoretical considerations than was the case in the earlier editions, and presents a new theory of the nature of the drive. A new final chapter summarizes the factors which influence the nature of the animal mind at various levels of development.

A fuller exposition of the general point of view from which this work is written will be found in my book, "Movement and Mental Imagery," published in 1916.

M. F. W.

VASSAR COLLEGE, POUGHKEEPSIE, N. Y.,
APRIL, 1926.

PREFACE TO THE FIRST EDITION

The title of this book might more appropriately, if not more concisely, have been "The Animal Mind as Deduced from Experimental Evidence." For the facts set forth in the following pages are very largely the results of the experimental method in comparative psychology. Thus many aspects of the animal mind, to the investigation of which experiment either has not yet been applied or is perhaps not adapted, are left wholly unconsidered. This limitation of the scope of the book is a consequence of its aim to supply what I have felt to be a chief need of comparative psychology at the present time. Although the science is still in its formative stage, the mass of experimental material that has been accumulating from the researches of physiologists and psychologists is already great, and is also for the most part inaccessible to the ordinary student, being widely scattered and to a considerable extent published in journals which the average college library does not contain. While we have books on animal instincts and on the interpretation of animal behavior, we have no book which adequately presents the simple facts.

Probably no bibliography seems to one who carefully examines it entirely consistent in what it includes and what it excludes. Certainly the one upon which this book is based contains inconsistencies. The design has been to exclude works bearing only upon general physiology, upon the morphology of the nervous system and sense organs, or upon the nature of animal instinct as such, and to include those which bear upon the topics mentioned in the chapter headings. Within these limits, the collection of references upon no topic is as full as would be necessary for the bibliography

of a special research upon that topic. Doubtless there are omissions for which no excuse can be found. In one or two cases, where the literature upon a single point is very large, as, for example, in the case of the function of the semicircular canals, only a few of the more important references have been given.

One further comment may be made. The book throughout deals with comparative rather than with genetic psychology.

I gratefully acknowledge help from a number of sources. To Professor Titchener I owe, not only my share of that genuine psychological spirit which he so successfully imparts to his pupils according to their ability, but various helpful criticisms upon the present work, about half of which he has read in manuscript. Dr. Yerkes has given me much invaluable aid in securing access to material, and has very kindly permitted me to see the proofs of his book on "The Dancing Mouse." As editor of the series he has reviewed my manuscript to its great advantage. Professors Georges Bohn and George H. Parker have showed especial courtesy in making their work accessible to me. Professor Jennings has kindly allowed the use of a number of illustrations from his book on "The Behavior of the Lower Organisms." My colleague Professor Aaron L. Treadwell has generously helped me in ways too numerous to specify. But perhaps my heaviest single obligation is to Professor I. Madison Bentley, who has read the manuscript of the entire book, and whose advice and criticism have been of the utmost benefit to every part of it.

M. F. W.

VASSAR COLLEGE,
OCTOBER 1, 1907.

PREFACE TO THE SECOND EDITION

The advance of comparative psychology during the past nine years has been remarkable. In preparing a second edition of this book I have tried to include every newly discovered fact of the first importance, but the literature is now so extensive that in order to keep the bibliography within reasonable limits, I have had to exercise more selection than I did in preparing the bibliography for the first edition. For like reasons, the text of the book does not enter so fully into detail in describing the results of a particular investigation as was possible when the material at hand was so much less in amount.

More than half the book has been completely rewritten, including the chapters on Vision, on Spatially Determined Reactions, and on The Modification of Conscious Processes by Individual Experience. I hope that the edition represents an advance upon its predecessor, not only by including many newly ascertained facts, but also by presenting its subject matter in more logical form.

M. F. W.

VASSAR COLLEGE,
APRIL, 1917.

TABLE OF CONTENTS

CHAPTER I

THE DIFFICULTIES AND METHODS OF COMPARATIVE PSYCHOLOGY .	PAGES 1-24
1. Difficulties. 2. Methods of Obtaining Facts: Anecdote. 3. Methods of Obtaining Facts: Experiment. 4. Methods of Obtaining Facts: the Ideal Method. 5. Methods of In- terpreting Facts.	

CHAPTER II

THE EVIDENCE OF MIND	25-33
6. Inferring Mind from Behavior. 7. Inferring Mind from Structure.	

CHAPTER III

THE MIND OF THE SIMPLEST ANIMALS	34-47
8. The Structure and Behavior of Amœba. 9. The Mind of Amœba.	

CHAPTER IV

DISCRIMINATION: METHODS OF INVESTIGATING IT	48-56
10. Preliminary Considerations. 11. Sense-organ Structure as Evidence of Discrimination. 12. Behavior as Evidence of Discrimination. 13. Evidence from Structure and Be- havior Combined. 14. Evidence for Discrimination of Cer- tain "Lower" Sensation Classes.	

CHAPTER V

SENSORY DISCRIMINATION: THE CHEMICAL SENSE	57-104
15. The Chemical Sense in Protozoa. 16. The Chemical Sense in Cœlenterates. 17. The Chemical Sense in Flat- worms. 18. The Chemical Sense in Annelids. 19. The Chemical Sense in Mollusks. 20. The Chemical Sense in Echinoderms. 21. The Chemical Sense in Crustacea. 22. The Chemical Sense in Arachnids. 23. The Chemical Sense in Insects. 24. How Ants Find Food. 25. The Use of Smell in Path-finding by Ants. 26. How Ants "Recognize" Nest Mates. 27. How Bees Are Attracted to Flowers. 28. How Bees Find the Hive. 29. How Bees "Recognize" Nest Mates. 30. The Chemical Sense in Vertebrates.	

CHAPTER VI

	PAGES
SENSORY DISCRIMINATION: HEARING	105-124

31. Hearing in Lower Invertebrates. 32. Hearing in Crustacea. 33. Hearing in Spiders. 34. Hearing in Insects. 35. Hearing in Fishes. 36. Hearing in Amphibia. 37. Hearing in Higher Vertebrates.

CHAPTER VII

SENSORY DISCRIMINATION: VISION	125-165
--	---------

38. Change of Light Intensity as a Stimulus. 39. The Continuous Action of Light: Photokinesis. 40. The Problem of Color Vision. 41. Methods of Investigating Color Vision: I. Methods Based on the Distribution of Physiological Intensity in the Spectrum. 42. II. Methods Based on Independent Variability of Reactions to Intensity and to Wave Length. 43. Summary of Results for Different Animal Forms. 44. Some Special Phenomena Connected with Visual Qualities.

CHAPTER VIII

SPATIALLY DETERMINED REACTIONS	166-212
--	---------

45. Classes of Spatially Determined Reactions. 46. Class I: Reactions to a Single Localized Stimulus. 47. Class II: Orienting Reactions; Possible Modes of Producing Them. 48. Orientation to Gravity: Protozoa. 49. Orientation to Gravity: Cœlenterates. 50. Orientation to Gravity: Planarians. 51. Orientation to Gravity: Annelids. 52. Orientation to Gravity: Mollusks. 53. Orientation to Gravity: Echinoderms. 54. Orientation to Gravity: Crustacea. 55. Orientation to Gravity: Spiders and Insects. 56. Orientation to Gravity: Vertebrates. 57. The Psychic Aspects of Orientation to Gravity. 58. Orientation to Light. 59. Influences Affecting the Sense of Light Orientations. 60. The Psychic Aspect of Orientation to Light. 61. Mutual Influence of Light and Gravity Orientations. 62. Orientation to Other Forces. 63. Class III: Reactions to a Moving Stimulus.

CHAPTER IX

SPACE PERCEPTION AND THE PERCEPTION OF THINGS	213-245
---	---------

64. Class IV: Reaction to an Image. 65. Methods of Investigating the Visual Image. 66. The Visual Perception of Size. 67. The Visual Perception of Form. 68. The Homing of Animals as Evidence of Image Vision. 69. Class V: Reactions Adapted to the Distance of Objects. 70. Tactual Space Perception. 71. Some Theoretical Considerations. 72. The Perception of Things.

TABLE OF CONTENTS

xiii

CHAPTER X

PAGES

THE MODIFICATION OF CONSCIOUS PROCESSES BY INDIVIDUAL EXPERIENCE	246-287
--	---------

73. Modifications Due to Essentially Temporary Physiological States: (a) Heightened Reaction as the Result of Previous Stimulation. 74. Modification Due to Essentially Temporary Physiological States: (b) Cessation of Reaction to a Repeated Slight Stimulus. 75. Modifications Due to Relatively Permanent Effects of Stimuli. 76. Learning Involving the Dropping Out of Movements. 77. The Formation of Systems of Successive Movements.

CHAPTER XI

THE MODIFICATION OF CONSCIOUS PROCESSES BY INDIVIDUAL EXPERIENCE (<i>Continued</i>)	288-337
---	---------

78. The Recognition of Landmarks. 79. The Memory Idea. 80. "Insight." 81. Conditions Favoring the Development of Memory Ideas. 82. Some Alleged Instances of Remarkable Mental Powers in Animals. 83. Certain General Conditions of Learning. 84. The General Theory of Learning.

CHAPTER XII

SOME ASPECTS OF ATTENTION	338-347
-------------------------------------	---------

85. The Interference of Stimuli. 86. Methods of Securing Prepotency of Vitally Important Stimuli. 87. The Peculiar Characteristics of Attention as a Device to Secure Prepotency.

CHAPTER XIII

THE ANIMAL MIND	348-355
---------------------------	---------

REFERENCES	357-418
----------------------	---------

INDEX OF SUBJECTS	419-426
-----------------------------	---------

INDEX OF NAMES	427-431
--------------------------	---------

THE ANIMAL MIND

THE ANIMAL MIND

CHAPTER I

THE DIFFICULTIES AND METHODS OF COMPARATIVE PSYCHOLOGY

§ 1. *Difficulties*

THAT the mind of each human being forms a region inac- /-
cessible to all save its possessor, is one of the commonplaces
of reflection. His neighbor's knowledge of each person's
mind must always be indirect, a matter of inference. How
wide of the truth this inference may be, even under the most
favorable circumstances, is also an affair of everyday ex-
perience: each of us can judge his fellow-men only on the
basis of his own thoughts and feelings in similar circum-
stances, and the individual peculiarities of different members
of the human species are of necessity very imperfectly com-
prehended by others. The science of human psychology has
to reckon with this unbridgeable gap between minds as its
chief difficulty. The psychologist may look into his own mind
and study its workings with impartial insight, yet he can
never be sure that the laws which he derives from such a study
are not distorted by some personal twist or bias. For example,
it has been suggested that the philosopher Hume was influ-
enced by his tendency toward a visual type of imagination in
his discussion of the nature of ideas, which to him were evi-
dently visual images. As is well known, the experimental
method in psychology has aimed to minimize the danger of
confusing individual peculiarities with general mental laws.

In a psychological experiment, an unbiased observer is asked to study his own experience under certain definite conditions, and to put it into words so that the experimenter may know what the contents of another mind are like in the circumstances. Thus language is an essential apparatus in experimental psychology; language with all its defects, its ambiguity, its substitution of crystallized concepts for the protean flux of actually lived experience, its lack of terms to express those parts of experience which are of small practical importance in everyday life, but which may be of the highest importance to mental science. Outside of the psychological laboratory language is not always the best guide to the contents of other minds, because it is not always the expression of a genuine wish to communicate thought. "Actions speak louder than words," the proverb says; but when words are backed by good faith they furnish by far the safest indication of the thought of others. Whether, however, our inferences are made on the basis of words or of actions, they are all necessarily made on the hypothesis that human minds are built on the same pattern, that what a given word or action would mean for my mind, this it means also for my neighbor's mind.

If this hypothesis be uncertain when applied to our fellow human beings, it fails us utterly when we turn to the lower animals. If my neighbor's mind is a mystery to me, how great is the mystery which looks out of the eyes of a dog, and how insoluble the problem presented by the mind of an invertebrate animal, an ant or a spider! We know that such minds must differ from ours not only in certain individual peculiarities, but in ways at whose nature we can only guess. The nervous systems of many animals vary widely from our own. We have, perhaps, too little knowledge about the functions of our own to conjecture with any certainty what difference this must make in the conscious life of such animals; but when we find sense organs, such as the compound eyes of insects or crustaceans, constructed on a plan wholly diverse

from that of ours; when we find organs apparently sensory in function, but so unlike our own that we cannot tell what purpose they serve,—we are baffled in our attempt to construct the mental life of the animals possessing them, for lack of power to supply the sensation elements of that life. “It is not,” said Locke, “in the power of the most exalted wit or enlarged understanding, by any quickness or variety of thought, to invent or frame one new simple idea in the mind” (584, Bk. II, ch. 2); we cannot imagine a color or a sound or a smell that we have never experienced; how much less the sensations of a sense radically different from any that we possess! Again, a bodily structure entirely unlike our own must create a background of organic sensation which renders the whole mental life of an animal foreign and unfamiliar to us. We speak, for example, of an “angry” wasp. Anger, in our own experience, is largely composed of sensations of quickened heart beat, of altered breathing, of muscular tension, of increased blood pressure in the head and face. The circulation of a wasp is fundamentally different from that of any vertebrate. The wasp does not breathe through lungs, it wears its skeleton on the outside, and it has the muscles attached to the inside of the skeleton. What is anger like in the wasp’s consciousness? We can form no adequate idea of it.

To this fundamental difficulty of the dissimilarity between animal minds and ours is added, of course, the obstacle that animals have no language in which to describe their experience to us. 2. Where this unlikeness is greatest, as in the case of invertebrate animals, language would be of little use since we could not interpret it from our experience; but the higher vertebrates could give us much insight into their minds if they could only speak. We are, however, restricted to the inferences we can draw from movements and sounds that are made for the most part without the intention of communicating anything to us. One happy consequence of this fact, which to a slight extent balances its disadvantages, is that

we have not to contend with self-consciousness and posing, which often invalidate human reports of introspection.

From these general considerations we can understand something of the special difficulties that beset the path of the comparative psychologist, who desires to know the contents of minds below the human level. Knowledge regarding the animal mind, like knowledge of human minds other than our own, must come by way of inference from behavior. Two fundamental questions then confront the comparative psychologist. First, by what method shall he find out how an animal behaves? Second, how shall he interpret the conscious aspect of that behavior?

§ 2. *Methods of Obtaining Facts: The Method of Anecdote*

The reading of such a book as Romanes's "Animal Intelligence," or of the letters about animal behavior in the *London Spectator*, will reveal one method of gathering information about what animals do. This has been termed the Method of Anecdote. It consists essentially in taking the report of another person regarding the action of an animal, observed most commonly by accident, and attracting attention because of its unusual character. In certain cases the observer while in engaged in some other pursuit happens to notice the singular behavior of an animal, and at his leisure writes out an account of it. In others, the animal is a pet, in whose high intellectual powers its master takes pride. It is safe to say that this method of collecting information always labors under at least one, and frequently under several, of the following disadvantages:—

1. The observer is not scientifically trained to distinguish what he sees from what he infers.
2. He is not intimately acquainted with the habits of the species to which the animal belongs.
3. He is not acquainted with the past experience of the individual animal concerned.

4. He has a personal affection for the animal concerned, and a desire to show its superior intelligence.

5. He has the desire, common to all humanity, to tell a good story.

Some of these tendencies to error it is unnecessary to illustrate. A good example of the dangers of (2), lack of acquaintance with the habits of the species, is given by Mr. and Mrs. Peckham. They quote the following anecdote reported by no less eminent and trained an observer than Wundt. "I had made myself," says that psychologist, "as a boy, a fly-trap like a pigeon cote. The flies were attracted by scattering sugar and caught as soon as they had entered the cage. Behind the trap was a second box separated from it by a sliding door, which could be opened or shut at pleasure. In this I had put a large garden spider. Cage and box were provided with glass windows on the top, so that I could quite well observe anything that was going on inside. . . . When some flies had been caught, and the slide was drawn out, the spider of course rushed upon her prey and devoured them. . . . This went on for some time. The spider was sometimes let into the cage, sometimes confined to her own box. But one day I made a notable discovery. During an absence the slide had been accidentally left open for some little while. When I came to shut it, I found that there was an unusual resistance. As I looked more closely, I found that the spider had drawn a large number of thick threads directly under the lifted door, and that these were preventing my closing it. . . ."

"What was going on in the spider's mind?" Wundt asks, and points out that it is unnecessary to assume that she understood and reasoned out the mechanical requirements of the situation. The whole matter can be explained, he thinks, in a simpler way. "I imagine that as the days went by there had been formed in the mind of the spider a determinate association on the one hand between free entry into the cage and the pleasurable feeling attending satisfaction of

the nutritive impulse, and on the other between the closed slide and the unpleasant feeling of hunger and inhibited impulse. Now in her free life the spider had always employed her web in the service of the nutritive impulse. Associations had therefore grown up between the definite positions of her web and definite peculiarities of the objects to which it was attached, as well as changes which it produced in the positions of certain of these objects,—leaves, small twigs, etc. The impression of the falling slide, that is, called up by association the idea of other objects similarly moved which had been held in their places by threads properly spun; and finally there were connected with this association the other two of pleasure and raising, unpleasantness and closing, of the door" (1085, pp. 351-352).

The Peckhams remark in criticism of this observation: "Had Wundt been familiar with the habits of spiders, he would have known that whenever they are confined they walk around and around the cage, leaving behind them lines of web. Of course many lines passed under his little sliding door, and when he came to close it there was a slight resistance. These are the facts. His inference that there was even a remotest intention on the part of his prisoner to hinder the movement of the door is entirely gratuitous. Even the simpler mental states that are supposed to have passed through the mind of the spider were the products of Wundt's own imagination" (783, p. 230). The fact that the anecdote was a recollection of childhood, so that it would probably be impossible to bring any evidence from the character of the web or other circumstance against the suggestion of Mr. and Mrs. Peckham, is a further instance of the unscientific use of anecdotal testimony.

An illustration of the third objection mentioned above, the disadvantage of ignorance of the animal's individual history, is furnished by Lloyd Morgan. In describing his futile efforts to teach a fox terrier the best way to pull a crooked stick through a fence, he says that the dog showed no sign

"of perceiving that by pushing the stick and freeing the crook he could pull the stick through. Each time the crook caught he pulled with all his strength, seizing the stick now at the end, now in the middle, and now near the crook. At length he seized the crook itself and with a wrench broke it off. A man who was passing . . . said, 'Clever dog that, sir; he knows where the hitch do lie.' The remark was the characteristic outcome of two minutes' chance observation" (703, pp. 142-143). How many anecdotes of animals are based on similar accidents?

It will be seen that in both the cases just criticised the error lies in the interpretation of the animal's behavior. Indeed, a root of evil in the method of anecdote consists in the fact that observation in this form is imperfectly divorced from interpretation. The maker of an anecdote is seldom content with merely telling one what the animal did and leaving future investigation and the comparative study of many facts to decide what the animal's conscious experience in doing it was like. The point of the anecdote usually consists in showing that a human interpretation of the animal's behavior is possible. Here is shown the desire to tell a good story, which we mentioned among the pitfalls of the anecdotal method; the wish to report something unusual, not to get a just conception of the normal behavior of an animal. As Thorndike has forcibly put it: "Dogs get lost hundreds of times and no one ever notices it or sends an account of it to a scientific magazine. But let one find his way from Brooklyn to Yonkers and the fact immediately becomes a circulating anecdote. Thousands of cats on thousands of occasions sit helplessly yowling, and no one takes thought of it or writes to his friend the professor; but let one cat claw at the knob of a door supposedly as a signal to be let out, and straightway this cat becomes the representative of the cat-mind in all the books" (963, p. 4).

All this is not to deny that much of the testimony to be found in Romanes's "Animal Intelligence" and Darwin's

"Descent of Man" is the trustworthy report of trained observers; but it is difficult to separate the grain from the chaff, and one feels toward many of the anecdotes the attitude of scepticism produced, for example, by this tale which an Australian lady reported to the Linnæan Society. The burial of some deceased comrades was accomplished, she says, by a nest of "soldier ants" near Sydney, in the following fashion. "All fell into rank walking regularly and slowly two by two, until they arrived at the spot where lay the dead bodies. . . . Two of the ants advanced and took up the dead body of one of their comrades; then two others, and so on until all were ready to march. First walked two ants bearing a body, then two without a burden; then two others with another dead ant, and so on, until the line was extended to about forty pairs, and the procession now moved slowly onward, followed by an irregular body of about two hundred ants. Occasionally the two laden ants stopped, and laying down the dead ant, it was taken up by the two walking unburdened behind them, and thus, by occasionally relieving each other, they arrived at a sandy spot near the sea." A separate grave was then dug for each dead ant. "Some six or seven of the ants had attempted to run off without performing their share of the task of digging; these were caught and brought back, when they were at once attacked by the body of ants and killed upon the spot. A single grave was quickly dug and they were all dropped into it." No funeral procession for them! Of this story Romanes says, "The observation seems to have been one about which there could scarcely have been a mistake" (872, p. 91). One is inclined to think it just possible that there was.

§ 3. *Methods of Obtaining Facts: The Method of Experiment*

Diametrically opposed to the Method of Anecdote and its unscientific character is the Method of Experiment. An experiment, properly conducted, always implies that the con-

ditions are controlled, or at least known; whereas ignorance of the conditions is, as we have seen, a common feature of anecdote. The experimenter is impartial; he has no desire to bring about any particular result. The teller of an anecdote wishes to prove animal intelligence. The experimenter is willing to report the facts precisely as he observes them, and is in no haste to make them prove anything. The conduct of an experiment upon an animal will, of course, vary according to the problem to be solved. If the object is to test some innate reaction on the animal's part, such as its ordinary responses to stimulation or its instincts, one need merely place the animal under favorable conditions for observation, make sure that it is not frightened or in an abnormal state, supply the appropriate stimulus unmixed with others, and watch the result. If it is desired to study the process by which an animal learns to adapt itself to a new situation, one must, of course, make sure in addition that the situation really is new to the animal, and yet that it makes sufficient appeal to some instinctive tendency to supply a motive for the learning process.

As one might expect, among the earliest experiments upon animals were those made by physiologists with a view to determining the functions of sense organs. The experimental movement in psychology was slow in extending itself into the field of the animal mind.

Romanes, whose adherence to the anecdotal method we have noted, made in 1881, rather as a physiologist than as a psychologist, a number of exact and highly valued experiments on coelenterates and echinoderms, which were summarized in his book entitled "Jelly-fish, Star-fish, and Sea-urchins," published in 1885. He has also recorded some rather informal experiments on the keenness of smell in dogs. Sir John Lubbock, in 1883, reported the results of some experiments on the color sense of the small crustacean *Daphnia*, and his book on "Ants, Bees, and Wasps," containing an account of experimental tests of the senses and "intelligence"

of these insects, appeared in the same year. A German entomologist, Vitus Graber, experimented very extensively at about this period on the senses of sight and smell in many animals. Preyer, the authority on child psychology, published in 1886 an experimental study of the behavior of the starfish. Loeb's work on the reactions of animals to stimulation began to appear in 1888. Max Verworn, the physiologist, published in 1889 an exhaustive experimental study of the behavior of single-celled animals. With the exception of Preyer and Romanes, all these men had but a secondary interest in comparative psychology. Lloyd Morgan, who has written instructively on comparative psychology, makes but a limited use of the experimental method. Wesley Mills, professor of physiology in McGill University, has studied very carefully the mental development of young animals such as cats and dogs, but is inclined to criticise the use of experiment in observing animals. The work of E. L. Thorndike, whose "Animal Intelligence" appeared in 1898, represents, perhaps, the first definite effect of the modern experimental movement in psychology upon the study of the animal mind. Thorndike's aim in this research was to place his animals (chicks, cats, and dogs) under the most rigidly controlled experimental conditions. The cats and dogs, reduced by fasting to a state of "utter hunger," were placed in boxes, with food outside, and the process whereby they learned to work the various mechanisms which let them out was carefully observed. Since the appearance of Thorndike's work the performance of experiments upon animals has played much part in the work of American psychological laboratories. It has been extensively undertaken also in those of Europe, but this is one experimental field in which America can claim priority of entry.

Despite the obvious advantages of experiment as a method for the study of animal behavior, it is not without its dangers. These were clearly stated by Wesley Mills in a criticism

of Thorndike's "Animal Intelligence" (681). They may be summed up by saying that there is a risk of placing the animal experimented upon under abnormal conditions in the attempt to make them definite and controllable.¹ Did not, for example, the extreme hunger to which Thorndike's cats and dogs were reduced, while it simplified the conditions in one sense by making the strength of the motive to escape as nearly as possible equal for all the animals, complicate matters in another sense by diminishing their capacity to learn? Were the animals perhaps frightened and distracted by the unusual character of their surroundings? Thorndike thinks not (966); but whether or no he succeeded in averting these dangers, it is clear that they are real. It is also obvious that they are the more threatening, the higher the animal with which one has to deal. Fright, bewilderment, loneliness, are conditions more apt to be met with among the higher vertebrates than lower down in the scale, and the utmost care should be taken to make sure that animals likely to be affected by them are thoroughly trained and at home in their surroundings before the experimenter records results.

§ 4. *Methods of Obtaining Facts: The Ideal Method*

The ideal method for the study of a higher animal involves patient observation upon a specimen known from birth, watched in its ordinary behavior and environment, and occasionally experimented upon with proper control of the conditions and without frightening it or otherwise rendering it abnormal. The observer should acquaint himself with the individual peculiarities of each animal studied, for there is no doubt that striking differences in mental capacity occur among the individuals of a single species. At the same time that he obtains the confidence of each individual animal, he should be able to hold in check the tendency to humanize it and to take a personal pleasure in its achievements if it be

¹ Cf. also Kline (542), and Vaschide and Rousseau (1005).

unusually endowed. This is, to say the least, not easy. Absolute indifference to the animals studied, if not so dangerous as doting affection, is yet to be avoided.

§ 5. *Methods of Interpreting Facts*

We may now turn from the problem of discovering the facts about animal behavior to the problem of interpreting them. If an animal behaves in a certain manner, what may we conclude the consciousness accompanying its behavior to be like? As we have seen, the interpretation is often confused with the observation, especially in the making of anecdotes; but theoretically the two problems are distinct. And at the outset of our discussion of the former, we are obliged to acknowledge that all psychic interpretation of animal behavior must be on the analogy of human experience. We do not know the meaning of such terms as perception, pleasure, fear, anger, visual sensation, etc., except as these processes form a part of the contents of our own minds. Whether we will or no, we must be anthropomorphic in the notions we form of what takes place in the mind of an animal. Accepting this fundamental proposition, the students of animals have yet differed widely in the conclusions they have drawn from it. Some have gone to the extreme of declaring that comparative psychology is therefore impossible. Others have joyfully hastened to make animals as human as they could. Still others have occupied an intermediate position.

Descartes and Montaigne are the two writers antedating the modern period who are most frequently quoted in this connection. The latter had evidently a natural sympathy with animals. In that most delightful twelfth chapter of the second book of *Essays*, "An Apology of Raymond Sebonde," he gives free rein to the inclination to humanize them. I quote Florio's translation: "The Swallowes which at the approach of spring time we see to pry, to search and ferret all the corners of our houses; is it without judgment

they seeke, or without discretion they chuse from out a thousand places, that which is fittest for them, to build their nests and lodging? . . . Would they (suppose you) first take water and then clay, unlesse they guessed that the hardnesse of the one is softened by the moistness of the other? . . . Why doth the spider spin her artificial web thicke in one place and thin in another? And now useth one, and then another knot, except she had an imaginary kind of deliberation, forethought, and conclusion?" To ascribe such behavior to the working of mere instinct, "with a kinde of unknowne, naturall and servile inclination," is unreasonable. "The Fox, which the inhabitants of Thrace use" to test the ice on a river before crossing, which listens to the roaring of the water underneath and so judges whether the ice is safe or not; "might not we lawfully judge that the same discourse possesseth her head as in like case it would ours? And that it is a kinde of debating reason and consequence, drawne from natural sense? 'Whatsoever maketh a noyse moveth, whatsoever moveth, is not frozen, whatsoever is not frozen, is liquid; whatsoever is liquid, yeelds under any weight?'" (691).

Descartes, on the other hand, writing some sixty years later, takes, as is well known, the opposite ground. He says in a letter to the Marquis of Newcastle, "As for the understanding or thought attributed by Montaigne and others to brutes, I cannot hold their opinion." While animals surpass us in certain actions, it is, he holds, only in those "which are not directed by thought. . . . They act by force of nature and by springs, like a clock, which tells better what the hour is than our judgment can inform us. And doubtless when swallows come in the spring, they act in that like clocks. All that honey bees do is of the same nature" (248, pp. 281-283). The statement of Descartes, contained in the letter to Mersenne of July 30, 1640, that animals are automata, is often misunderstood. Descartes does not assert that animals are unconscious in the sense which that term would carry to-day, but only that they are without thought. Sensations, feel-

ings, passions, he is willing to ascribe to them, in so far as these do not involve thought. "It must however be observed that I speak of thought, not of life, nor of sensation," he says in the letter to Henry More, 1649; "I do not refuse to them feeling . . . in so far as it depends only on the bodily organs" (248, p. 287). In this he does not go so far as some modern writers, who decline to assert the presence of any psychic process in the lower forms of animal life.

Turning to recent times, we find arguments very like those of Montaigne used by the earlier evolutionary writers. Darwin, for instance, says in "The Descent of Man," "As dogs, cats, horses, and probably all the higher animals, even birds, have vivid dreams, and this is shown by their movements and the sounds uttered, we must admit that they possess some power of imagination" (227, p. 74). "Even brute beasts," says Montaigne, ". . . are seen to be subject to the power of imagination; witness some Dogs . . . whom we ordinarily see to startle and barke in their sleep" (694, Bk. I, ch. 20). "Only a few persons," Darwin continues, "now dispute that animals possess some power of reasoning. Animals may constantly be seen to pause, deliberate, and resolve." And he states that his object in the third chapter of the work quoted is "to show that there is no fundamental difference between man and the higher mammals in their mental faculties" (227, p. 66). Romanes is evidently guided by the same desire to humanize animals.

Now these writers were not led to take such an attitude merely out of general sympathy with the brute creation, like Montaigne; they had an ulterior motive; namely, to meet the objection raised in their time against the doctrine of evolution, based on the supposed fact of a great mental and moral gulf between man and the lower animals. They wished to show, as Darwin clearly states, that this gulf is not absolute but may conceivably have been bridged by intermediate stages of mental and moral development. While this argument against evolution was being pressed, the evolutionary writers

were very unsafe guides in the field of animal psychology, for they distinctly "held a brief for animal intelligence," to use Thorndike's phrase. In more recent times interest in both the positive and the negative sides of the objection drawn from man's superiority has died out, and such special pleading has become unnecessary.

On the other hand, the fact that the greater part of the experiments on animals were until the last twenty-five years performed by physiologists has given rise to an opposite tendency in interpreting the animal mind: the tendency to make purely biological concepts suffice as far as possible for the explanation of animal behavior and to assume the presence even of consciousness in animals only when it is absolutely necessary to do so. Loeb in 1890 suggested the theory which he has since elaborated, that the responses of animals to stimulation, instead of being signs of "sensation," are in every way analogous to the reactions of plants to such forces as light and gravity; hence unconscious "tropisms" (587). Bethe in 1898 attempted to explain all the complicated behavior of ants and bees, which the humanizing writers had compared with our own civilization, as a result of reflex responses, chiefly to chemical stimulation, unaccompanied by any consciousness whatever (61). This revival, in an altered form, of the Cartesian doctrine has met with energetic opposition, especially from writers having philosophical interests. When the first edition of the present work appeared, the parties in the controversy could be divided into three groups: those who believed that consciousness should be ascribed to all animals; those who believed that it should be ascribed only to those animals whose behavior presents certain peculiarities regarded as evidence of mind; and those who held that we have no trustworthy evidence of mind in any animal, and should therefore abandon comparative psychology and use only physiological terms. Of recent years, the tendency has been towards the survival only of the two extreme parties: it has been more and more recognized that there exists no evi-

dence of mind which is not either equally bad or equally good in the case of all animals.

Among the authorities who would ascribe mind to all animals belong Claparède of Geneva, the Swiss naturalist Forel, and the Jesuit Wasmann. They maintain this position from widely different philosophical points of view. The first-named is what is called a parallelist; that is, he believes that mental processes and bodily processes are not causally related, but form two parallel and non-interfering series of events. In the study of animals, both the physical and the psychical series should, he thinks, be investigated. Biology should use two parallel methods, the one ascending, attempting to explain animal behavior by physical and chemical laws; the other descending, giving an account of the mental processes of animals. Ultimately, it may be hoped, according to Claparède, that both methods will be applied throughout the whole range of animal life. At present the ascending method is most successful with the lowest forms, the descending method with the highest forms. We cannot afford to abandon the psychological study of animals, for our knowledge of the nervous processes underlying the higher mental activities is very slight; physiology here fails us, and psychology must be left in command of the field. The danger besetting the attempt at a purely physical explanation of animal behavior is that the facts shall be unduly simplified to fit the theory. Thus Bethe's effort at explaining the way in which bees find their way back to the hive as a reflex response, or tropism, produced by "an unknown force," is highly questionable; the facts seem to point toward the exercise of some sort of memory by the bees. It is always possible, further, that the tropism is accompanied by consciousness. A physiologist from Saturn might reduce all human activities to tropisms, says Claparède in a striking passage. "The youth who feels himself drawn to medical studies, or he who is attracted to botany, can no more account for his profoundest aspirations than the beetle which runs to the odor of a dead animal or the butter-

fly invited by the flowers; and if the first shows a certain feeling corresponding to these secret states of the organism (a feeling of 'predilection' for such a career, etc.), how can we dare to deny to the second analogous states of consciousness?" (168). If it is argued that we have no direct, but only an inferential, knowledge of the processes in an animal's mind, the argument is equally valid against human psychology, for the psychologist has only an inferential knowledge of his neighbor's mind (170).

Wasmann defends the animal mind from a different position. For one thing, he believes that mental processes may act causally upon bodily states. He accepts, in other words, what is called interactionism, as opposed to parallelism. Further, although he strongly opposes the doctrine that the reactions of animals are unconscious tropisms and constantly emphasizes their variability and modifiability through experience, he nevertheless believes that a gulf separates the human from the animal mind. The term "intelligence" which most writers use to designate merely the power of learning by individual experience, Wasmann would reserve for the power of deducing and understanding relations and would assign only to human beings (1038, 1039). Although animals have their instincts modified by sense experience, man "stands through his reason and freedom immeasurably high above the irrational animal that follows, and must follow, its sensuous impulse without deliberation" (1040).

Forel, in the third place, is what is called a monist in metaphysics. That is, he does not believe either that mind and body are parallel, or that they interact causally, but that they are two aspects of the same reality. "Every psychic phenomenon is the same real thing as the molecular or neuro-cymic activity of the brain-cortex coinciding with it" (310 p. 7). The psychic and the physical, on this theory, should be coextensive; not merely should consciousness in some form belong to all living things, but every atom of matter should have its psychic aspect. On such a basis, Forel takes highly

Part of a monism in metaphysics

optimistic views of the animal mind. In insects, of which he has made a special study, it is, he thinks, "possible to demonstrate the existence of memory, associations of sensory images, perceptions, attention, habits, simple powers of inference from analogy, the utilization of individual experience, and hence distinct, though feeble, plastic individual deliberations or adaptations" (310, p. 36).

A peculiar position on the problem of mind in animals is occupied by the "vitalists," of whom Driesch (260) is the foremost representative. They regard the reactions of organisms as requiring the operation of psychic forces or "entelechies"; they hold that as physical phenomena such reactions cannot be explained save through the working of these psychic forces. A living being is forever distinguished from a lifeless creature by the presence of such entelechies. Thus the vitalist is an interactionist and a dualist: the worlds of the lifeless and the living are to him forever distinct. The vitalistic position in comparative psychology is defended by W. McDougall (624). It involves abandoning all attempt to explain the mind of animals by reference to underlying physiological processes; maintaining that conscious purpose is involved in instinctive as well as in intelligent action, and assuming, as a result of this belief, that a bird, for example, building its first nest, is guided by an innate idea of the pattern.

The opposite camp is represented by Bethe, Beer, von Uexküll, Loeb, and other physiologists, as well as by Watson.

The eminent neurologist Bethe, in his study of the behavior of ants and bees, refuses to allow these animals any "psychic qualities" whatever, and suggests the term "chemo-reception" instead of "smell," to designate the influence which directs most of their reactions,— "smell" implying a psychic quality (61). In a footnote to a later article he says: "Psychic qualities cannot be demonstrated. Even what we call sensation is known to each man only in himself, since it is something subjective. We possess the capacity of modifying our behavior [i.e., of learning], and every one knows from his

own experience that psychic qualities play a part connected with this modifying process. Every statement that another being possesses psychic qualities is a conclusion from analogy, not a certainty; it is a matter of faith. If one wishes to draw this analogical inference, it should be made where the capacity for modification can be shown. When this is lacking, there is not the slightest scientific justification for assuming psychic qualities. They *may* exist, but there is no probability of it, and hence science should deny them. Hence if one ventures to speak of a Psyche in animals at all, one should give the preference to those which can modify their behavior" (61). But that Bethe himself prefers not to make the venture is evident from statements in the text of the same article. The psychic or subjective, he says, is unknowable, and the only thing we may hope to know anything about is the chemical and the physiological processes involved. "These chemo-physical processes and their consequences, that is, the objective aspect of psychic phenomena, and these alone, should be the object of scientific investigation" (61).

Together with Beer and von Uexküll, Bethe shortly afterward published "Proposals for an Objectifying Nomenclature in the Physiology of the Nervous System." The main purpose of this paper was to suggest that all terms having a psychological implication, such as sight, smell, sense-organ, memory, learning, and the like, be carefully excluded from discussions of animal reactions to stimulation and animal behavior generally. In their stead the authors propose such expressions as the following: for responses to stimulation where no nervous system exists, the term *antitypes*; for those involving a nervous system, *antikineses*; the latter are divided into *reflexes*, where the response is uniform, and *antiklises*, where the response is modifiable. A sense-organ becomes a *reception-organ*, sensory nerves are *receptory-nerves*, and we have *phono-reception*, *stibo-reception*, *photo-reception*, instead of hearing, smell, and sight. The after-effect of a stimulus upon later ones is the *resonance* of the stimulus (48).

Now
nomenclature
suggested
by Beer
& von Uexküll

action of mechanists

Loeb (600) agrees with Bethe that physico-chemical processes and not states of consciousness are the proper objects of investigation for the "psychologist." These men evidently regard the universe as essentially uniform throughout—there exists for them no gulf between living and lifeless things; the behavior of living beings will be reduced to a series of chemical reactions as soon as science has progressed sufficiently far. They are "mechanists." It is, however, perfectly possible to be a mechanist so far as the explanation of animal behavior is concerned, and still admit that animals have consciousness and that their behavior is accompanied by inner, mental states which it is the business of the psychologist to investigate. One does not have to be a vitalist to believe that animals have minds: one may hold that every action of an animal will some day be explained as the result of physico-chemical processes, and yet maintain that the actions of animals are conscious. The consciousness would be an accompaniment, an inner aspect, of the physico-chemical processes.

action of behaviorists

The views of Loeb and Bethe have gained much ground lately among certain American psychologists, notably Watson (1049). The position of these "behaviorists" seems not to have been fully thought out in its philosophical aspects, but is somewhat as follows. The difficulties of interpreting an animal's mind from its behavior are so great that such inferences have no scientific value. We may therefore proceed as if animals had no minds; or rather, as if mind were a kind of behavior, observable by outside means. Since it is obvious that the difficulty of interpreting an animal's mind from its behavior is only greater in degree than, not unlike in kind, the difficulty of interpreting other human minds from behavior, human psychology also should confine itself to the observation merely of the actions of other persons, and permit no inferences as to the inner aspect of such actions. In fact, there is no inner aspect to such actions—thoughts and feelings, human as well as animal, are only behavior, and if we have at present no instruments for inspecting and measur-

ing the movements which are thoughts and feelings, such instruments will in time be discovered.

In opposition to these views, we shall in this book maintain the following position. There exists an inner aspect to behavior, the realm of sensations, feelings, and thoughts, which is not itself identical with behavior or with any form of movement. Thoughts probably always have as their accompaniment bodily movements, but the thought is not identical with the movement. If a physiologist perfected an instrument by which he could observe the nervous process in my cortex that occurs when I am conscious of the sensation red, he would see nothing red about it; if he could watch the bodily movements that result from this stimulation, say, for instance, the slight contraction of the articulatory muscles that occurs when I say "red" to myself, he would not see them as red. The red is in my consciousness, and no devices for observing and registering my movements will ever observe the red, though they may easily lead to the inference that it exists in my consciousness. And precisely the same is true of all my sensations, thoughts, and feelings.

*action
movement*

Since an inner world of experience exists, we may legitimately try to investigate it. For this purpose we possess a method, which is called introspection. We can, that is, attentively and, if we have had practice, dispassionately and scientifically, observe what goes on in our own consciousness when we receive certain stimuli and make certain movements. Further, we can by the use of the same kind of inference from one case to another similar case, upon which all scientific generalization is based, infer that when a being whose structure resembles ours receives the same stimulus that affects us and moves in the same way as a result, he has an inner experience which resembles our own. Finally, we may extend this inference to the lower animals, with proper safeguards, just as far as they present resemblances in structure and behavior to ourselves. One main object in this book will be the interpretation of the inner aspect of the behavior

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of animals; we shall be interested in what animals do largely as it throws light upon what they feel. To the true psychologist, no challenge is so enticing as that presented by the problem of how it feels to be another person or another animal; and although we must sometimes give up the problem in despair, yet we have also our successes. We have wonderfully advanced, within the last twenty-five years, in knowledge as to how the world looks from the point of view of our brother animals.

precautions in interpreting on off conscious aspect of animal behavior

We may now note briefly some of the special precautions that must be observed in interpreting the conscious aspect of animal behavior. First, there is no doubt that great caution should be used in regarding the quality of a human conscious process as identical with the quality of the corresponding process in the animal mind. For example, we might say with a fair degree of assurance that an animal consciously discriminates between light and darkness; that is, receives conscious impressions of different quality from the two, yet the mental impression produced by white light upon the animal may be very different from the sensation of white as we know it, and the impression produced by the absence of light very different from our sensation of black. Black and white may, for all we know, depend for their quality upon some substance existing only in the human retina. Yet where there is resemblance both in sense-organ structure and in discriminative behavior, the possibility of unlikeness in sensation quality becomes too remote to be interesting.

and organ's canon

A second precaution concerns the simplicity or complexity of the interpretation put upon animal behavior. Lloyd Morgan, in his "Introduction to Comparative Psychology," formulated a conservative principle of interpretation which has often been quoted as "Lloyd Morgan's Canon." The principle is as follows: "In no case may we interpret an action as the outcome of the exercise of a higher psychological faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale" (701, p. 53). In

other words, when in doubt take the simpler interpretation. For example, a dog detected in a theft cowers and whines. One possible mental accompaniment of this behavior is remorse; the dog is conscious that he has fallen below a moral standard, and grieved or offended his master. A second is the anticipation of punishment; the dog has a mental representation of the consequences of his action upon former occasions, and imagining himself likely to experience them anew, is terrified at the prospect. A third possibility is that the dog's previous experience of punishment, instead of being revived in the form of definite images, makes itself effective merely in his feelings and behavior; he is uncomfortable and frightened, he knows not definitely why. It is evident that these three possibilities represent three different grades of complexity of mental process, the first being by far the highest. Lloyd Morgan's canon enjoins upon us in such a case to prefer the third alternative, provided that it will really account for the dog's behavior.

Now why should the simplest interpretation be preferred? We must not forget that the more complex ones remain in the field of possibility. Dogmatic assertions have no place in comparative psychology. We cannot say that the simplicity of an hypothesis is sufficient warrant of its truth, for nature does not always proceed by the paths which seem to us least complicated. The fact is that Lloyd Morgan's principle serves to counterbalance our most important source of error in interpreting animal behavior. It is like tipping a boat in one direction to compensate for the fact that some one is pulling the opposite gunwale. We must interpret the animal mind humanly if we are to interpret it at all. Yet we know that it differs from the human mind, and that the difference is partly a matter of complexity. Let us therefore take the least complex interpretation that the facts of animal behavior will admit, always remembering that we may be wrong in so doing, but resting assured that we are, upon the whole, on the safer side. The social consciousness of man is very strong,

and his tendency to think of other creatures, even of inanimate nature, as sharing his own thoughts and feelings, has shown itself in his past to be almost irresistible. Lloyd Morgan's canon offers the best safeguard against this natural inclination, short of abandoning all attempt to study the mental life of the lower animals.

CHAPTER II

THE EVIDENCE OF MIND

§ 6. *Inferring Mind from Behavior*

IN this chapter we shall try to show that there exists no evidence for denying mind to any animals, if we do not deny it to all; in other words, that there is no such thing as an objective proof of the presence of mind, whose absence may be regarded as proof of the absence of mind.

To begin with, can it be said that when an animal makes a movement in response to a certain stimulus, there is an accompanying consciousness of the stimulus, and that when it fails to move, there is no consciousness? Is response to stimulation evidence of consciousness? In the case of man, we know that absence of visible response does not prove that the stimulus has not been sensed; while it is probable that some effect upon motor channels always occurs when consciousness accompanies stimulation, the effect may not be apparent to an outside observer. On the other hand, if movement in response to the impact of a physical force is evidence of consciousness, then the ball which falls under the influence of gravity and rebounds on striking the floor is conscious. Nor is the case improved if we point out that the movements which animals make in response to stimulation are not the equivalent in energy of the stimulus applied, but involve the setting free of energy stored in the animal as well. True, when a microscopic animal meets an obstacle in its swimming, and darts backward, the movement is not a mere rebound; it implies energy contributed by the animal's own body. But just so an explosion of gunpowder is not the equivalent in energy of the heat of the match, the stimulus.

Similarly it is possible to think of the response made by animals to external stimuli as involving nothing more than certain physical and chemical processes identical with those existing in inanimate nature.

2. If we find that the movements made by an animal as a result of external stimulation regularly involve withdrawal from certain stimuli and acceptance of others, it is natural to use the term "*choice*" in describing such behavior. But if consciousness is supposed to accompany the exercise of choice in this sense, then consciousness must be assumed to accompany the behavior of ions in chemical combinations. When hydrochloric acid is added to a solution of silver nitrate, the ions of chlorine and those of silver find each other by an unerring "*instinct*" and combine into the white precipitate of silver chloride, while the hydrogen and the nitric acid similarly "*choose*" each other. Nor can the fact that behavior in animals is adapted to an end be used as evidence of mind; for "*purposive*" reactions, which contribute to the welfare of an organism, are themselves selective. The search for food, the care for the young, and the complex activities which further welfare, are made up of reactions involving "*choice*" between stimuli; and if the simple "*choice*" reaction is on a par with the behavior of chemical ions, so far as proof of consciousness goes, then *adaptation to an end*, apparent purposiveness, is in a similar position.

3. Thus the mere fact that an animal reacts to stimulation, even selectively and for its own best interests, offers no evidence for the existence of mind that does not apply equally well to particles of inanimate matter. Moreover, there is some ground for holding that the reactions of the lowest animals are unconscious. This ground consists in the apparent lack of variability which characterizes such reactions. In our own case, we know that certain bodily movements, those of digestion and circulation, for example, are normally carried on without accompanying consciousness, and that in other cases where there is consciousness of the stimulus, as in the

reflex knee-jerk, it occurs after the movement is initiated, so that the nervous process underlying the sensation would seem to be immaterial to the performance of the movement. These unconscious reactions in human beings are characterized by their relative uniformity, by the absence of variation in their performance. Moreover, when an action originally accompanied by consciousness is often repeated, it tends, by what is apparently one and the same process, to become unconscious and to become uniform. There is consequently reason for believing that when the behavior of lower animals displays perfect uniformity, consciousness is not present. On the other hand, an important reservation must be made in the use of this negative test. It is by no means easy to be sure that an animal's reactions are uniform. The more carefully the complex ones are studied, the more are variability and difference brought to light where superficial observation had revealed a mechanical and automatic regularity. It is quite possible that even in the simple, apparently fixed response of microscopic animals to stimulation, better facilities for observation might show variations that do not now appear.

This matter of uniformity *versus* variability suggests a further step in our search for a satisfactory test of the presence of mind. Is mere *variability* in behavior, mere irregularity in response, to be taken as such a test? Not if we argue from our own experience. While that portion of our own behavior which involves consciousness shows more irregularity than the portion which does not, yet the causes of the irregularity are often clearly to be found in physiological conditions with which consciousness has nothing to do. There are days when we can think clearly and recall easily, and days when obscurities refuse to vanish and the right word refuses to come; days when we are irritable and days when we are sluggish. Yet since we can find nothing in our mental processes to account for this variability, it would be absurd to take analogous fluctuations in animal behavior as evidence of mind. So complicated a machine as an animal

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organism, even if it be nothing more than a machine, must show irregularities in its working.

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criteria* Behavior, then, must be variable, but not merely variable, to give evidence of mind. The criterion most frequently applied to determine the presence or absence of the psychic is a variation in behavior that shows definitely the result of previous individual experience. "Does the organism," says Romanes, "learn to make new adjustments, or to modify old ones, in accordance with the results of its own individual experience?" (873, p. 4). Loeb declared that "the fundamental process which occurs in all psychic phenomena as the elemental component" is "the activity of the associative memory, or of association," and defines associative memory as "that mechanism by which a stimulus brings about not only the effects which its nature and the specific structure of the irritable organ call for, but by which it brings about also the effects of other stimuli which formerly acted upon the organism almost or quite simultaneously with the stimulus in question." "If an animal can be trained," he continued, "if it can learn, it possesses associative memory," and therefore mind (595, p. 12). The psychologist finds the term "associative memory" hardly satisfactory, and objects to the confusion between mental and physical concepts which renders it possible to speak of a "mechanism" as forming an "elemental component" in "psychic phenomena," but these points may be passed over. The power to learn by individual experience is the evidence which Romanes, Morgan, and Loeb will accept as demonstrating the presence of mind in an animal.

Does the absence of proof that an animal learns by experience show that the animal is unconscious? Romanes is careful to answer this question in the negative. "Because a lowly organized animal," he says, "does *not* learn by its own individual experience, we may not therefore conclude that in performing its natural or ancestral adaptations to appropriate stimuli, consciousness, or the mind element, is wholly absent; we can only say that this element, if present,

reveals no evidence of the fact" (873, p. 3). Loeb, on the other hand, wrote as if absence of proof for consciousness amounted to disproof, evidently relying on the principle of parsimony, that no unnecessary assumptions should be admitted. "Our criterion," he remarked, "puts an end to the metaphysical ideas that all matter, and hence the whole animal world, possesses consciousness" (595, p. 13). If learning by experience be really a satisfactory proof of mind, then its absence in certain animals would indeed prevent the positive assertion that all animals are conscious; but it could not abolish the possibility that they might be. Such a possibility might, however, be of no more scientific interest than any one of a million wild possibilities that science cannot spare time to disprove. But we shall find that learning by experience, taken by itself, is too indefinite a concept to be of much service, and that when defined, it is inadequate to bear the whole weight of proving consciousness in animals. Such being the case, the possibility that animals which have not been shown to learn may yet be conscious acquires the right to be reckoned with.

The first point that strikes us in examining the proposed test is that the learning by experience must not be too slow, or we can find parallels for it in the inanimate world. An animal may be said to have learned by experience if it behaves differently to a stimulus because of preceding stimuli. But it is one thing to have behavior altered by a single preceding stimulus, and another to have it altered by two hundred repetitions of a stimulus. The wood of a violin reacts differently to the vibrations of the strings after it has "experienced" them for ten years; the molecules of the wood have gradually taken on an altered arrangement. A steel rail reacts differently to the pounding of wheels after that process has been long continued; it may snap under the strain. Shall we say that the violin and the rail have learned by individual experience? If the obvious retort be made that it is only in living creatures that learning by experience should be taken

as evidence of mind, let us take an example from living creatures. When a blacksmith has been practising his trade for a year, the reactions of his muscles are different from what they were at the outset. But this difference is not merely a matter of more accurate sense-discrimination, a better "placing" of attention and the like; there have been going on within the structure of his muscles changes which have increased their efficiency, and with which consciousness has had nothing to do. These changes have been extremely slow compared to the learning which does involve consciousness. In one or two lessons the apprentice learned what he was to do; but only very gradually have his muscles acquired the strength to do it as it should be done. Now among the lower animal forms we sometimes meet with learning by experience that is very slow; that requires a hundred or more repetitions of the stimulus before the new reaction is acquired. In such a case we can find analogical reasons for suspecting that a gradual change in the tissues of the body has taken place, of the sort which, like the attuning of the violin wood or the slow development of a muscle, have no conscious accompaniment.

We must then ask the question: What kind of learning by experience never, so far as we know, occurs unconsciously? Suppose a human being shut up in a room from which he can escape only by working a combination lock. As we shall see later, this is one of the methods by which the learning power of animals has been tested. The man, after prolonged investigation, hits upon the right combination and gets out. Suppose that he later finds himself again in the same predicament, and that without hesitation or fumbling he opens the lock at once, and performs the feat again and again, to show that it was not a lucky accident. But one interpretation of such behavior is possible. We know from our own experience that the man could not have worked the lock the second time he saw it, unless he consciously remembered the movements he made the first time; that is, unless he had in mind some

kind of idea as a guide. Here, at least, there can have been no change in the structure of the muscles, for such changes are gradual; the change must have taken place in the most easily alterable portion of the organism, the nervous system; and further, it must have taken place in the most unstable and variable part of the nervous system, the higher cortical centres whose activity is accompanied by consciousness. In other words, we may be practically assured that consciousness accompanies learning only when the learning is so rapid as to show that the effects of previous experience are recalled in the guise of an idea or mental image of some sort. But does even the most rapid learning possible assure us of the presence of an idea in the mind of a lower animal? Where the motive, the beneficial or harmful consequence of action, is very strong, may not a single experience suffice to modify action without being revived in idea? Moreover, animals as high in the scale as dogs and cats learn to solve problems analogous to that of the combination lock so slowly that we cannot infer the presence of ideas. Are we then to conclude that these animals are unconscious, or that there is absolutely no reason for supposing them possessed of consciousness? Yerkes has criticised the "learning by experience" criterion by pointing out that "no organism . . . has thus far been proved incapable of profiting by experience." It is a question rather of the rapidity and of the kind of learning involved. "The fact that the crayfish needs a hundred or more experiences for the learning of a type of reaction that the frog would learn with twenty experiences, the dog with five, say, and the human subject with perhaps a single experience, is indicative of the fundamental difficulty in the use of this sign" (1106). Nagel has pointed out that Loeb, in asserting "associative memory" as the criterion of consciousness, offers no evidence for his statement (724). The fact is that while proof of the existence of mind can be derived from animal learning by experience only if the learning is very rapid, other evidence, equally valid on the principle of analogy, makes it *highly improbable*

that all animals which learn too slowly to evince the presence of ideas are therefore unconscious. This evidence is of a morphological character.

§ 7. *Inferring Mind from Structure*

Both Yerkes and Lukas urge that the resemblance of an animal's nervous system and sense organs to those of human beings ought to be taken into consideration in deciding whether the animal is conscious or not. Lukas suggests that the criteria of consciousness should be grouped under three heads: morphological, including the structure of the brain and sense-organs, physiological, and teleological. Under the second rubric he maintains that "individual purposiveness" is characteristic of the movements from which consciousness may be inferred; that individual purposiveness pertains only to voluntary acts, and that voluntary acts are acts "which are preceded by the intention to perform a definite movement, hence by the idea of this movement." We have reached the same conclusion in the preceding paragraph. The third test of the presence of consciousness, the teleological test, rests on the consideration: "What significance for the organism may be possessed by the production of a conscious effect by certain stimuli?" (613). This test, however, being of a purely *a priori* character, would seem to be distinctly less valuable than the others.

Yerkes proposes "the following six criteria in what seems to me in general the order of increasing importance. The functional signs are of greater value as a rule than the structural; and within each of the categories the particular sign is usually of more value than the general. In certain cases, however, it might be maintained that neural specialization is of greater importance than modifiability.

I. Structural Criteria.

1. General form of organism (Organization).
2. Nervous system (Neural organization).

3. Specialization in the nervous system (Neural specialization).

II. Functional Criteria.

1. General form of reaction (Discrimination).
2. Modifiability of reaction (Docility).
3. Variability of reaction (Initiative)" (1106).

The terms "discrimination," "docility," and "initiative" in this connection are borrowed from Royce's "Outlines of Psychology" (884).

If resemblance of nervous and sense-organ structure to the human type is to be taken along with rapid learning as co-ordinate evidence of consciousness, it is clear that here also we have to deal with a matter of degree. The structure of the lower animals differs increasingly from our own as we go down the scale. At what degree of difference shall we draw the line and say that the animals above it may be conscious, but that those below it cannot be? No one could possibly establish such a line. The truth of the whole matter seems to be this: We can say neither what amount of resemblance in structure to human beings, nor what speed of learning, constitutes a definite mark distinguishing animals with minds from those without minds, unless we are prepared to assert that only animals which learn so fast that they must have memory ideas possess mind at all. And this would conflict with the argument from structure. For example, there is no good experimental evidence that cats possess ideas, yet there is enough analogy between their nervous systems and our own to make it improbable that consciousness, so complex and highly developed in us, is in them wholly lacking. We know not where consciousness begins in the animal world. We know where it surely resides—in ourselves; we know where it exists beyond a reasonable doubt—in those animals of structure resembling ours which rapidly adapt themselves to the lessons of experience. Beyond this point, for all we know, it may exist in simpler and simpler forms until we reach the very lowest of living beings.

CHAPTER III

THE MIND OF THE SIMPLEST ANIMALS

§ 8. *The Structure and Behavior of Amœba*

WE have seen in the last chapter that no one can prove the absence of consciousness in even the simplest forms of living beings. It is therefore perfectly allowable to speculate as to what may be the nature of such consciousness, provided that the primitive organisms concerned possess it. Perfectly allowable, yet also perfectly useless, many authorities would argue; the remoteness of the creatures from ourselves in structure and behavior renders theorizing about their conscious experience, which is probably non-existent and certainly unimaginable in any definite terms by us, the idlest form of mental exercise.

Undeniably the formation of a positive notion regarding the character and content of psychic states in the mind, say of an Amœba, is next door to an impossibility. Yet it may not be wholly a waste of time if we spend a few pages in the attempt to discover wherein the simplest type of mind, supposing it to be that belonging to the simplest type of animal, necessarily differs from our own. Some light, perhaps, may be cast upon the growth of mental life in complexity if we try to make clear to ourselves what primitive consciousness is not, though we may not be able to find in our own experience any elements that shall properly represent what it is.

The first need is evidently information about the structure and the behavior of a primitive animal. For this purpose the Amœba presents itself as a good subject. Structurally, it consists of a single cell, as do all the Protozoa, the lowest group of animals; it is so small that it can be studied only through the microscope; its form, at least that of *Amœba proteus*, the most

typical species, is irregular and constantly changing in locomotion or in response to stimulation. While the internal substance of its body shows a certain amount of differentiation, there is no trace whatever of special modifications that might be supposed to serve for the conduction of stimuli to different parts of the body, and thus represent the prototype of a nervous system. Nor have any structures been found that could conceivably be used for the special reception of stimuli; that is, there are no sense organs. So far as the anatomy of the animal is concerned, then, it differs so widely from our own that we could only conclude from it the absence of all those features which our conscious experience involves.

Turning from structure to behavior, we find the external activities of *Amœba*, that is, those not confined to the inner processes of its cell body, to be superficially, at least, divisible into two classes: movements of locomotion and responses to stimulation. *Amœba*, though a water-dwelling animal, is not a free-swimming one, but moves by crawling on a solid body. This method of locomotion involves in *Amœba proteus* changes of form on the animal's part, projections, called pseudopodia, being sent out in advance of the movement of the whole body. The protoplasm of the body shows in this process certain flowing movements which are differently described by different observers, and doubtless vary in different species: thus Rhumbler finds that the protoplasmic currents move backward along the sides of the animal and forward through the middle in a way quite comparable to the behavior of currents in a drop of any fluid where the tension of the surface is diminished in front, *i.e.*, at the point toward which the drop, in consequence of the diminished tension there, rolls. Such movements, Rhumbler shows, can be reproduced by placing, say, a drop of clove oil under the proper conditions of surface tension (861, 862). Jennings, on the other hand, has observed, at least in certain species of *Amœba*, that the protoplasmic currents are all forward in direction, the movement being really one of rolling, complicated by the attachment of the lower part of

the body to the solid object on which the animal crawls. Mechanical conditions of surface tension would not account for such currents (505, 507, 512). Dellinger rejects both the surface tension and the "rolling" theories, and from a study of side views of the moving *Amœba* concludes that progression occurs through the advancement of the front end freely through the water and its subsequent attachment, the rest of the body following through active contraction brought about by a contractile substance (245). The problem is of great interest to the student of vital phenomena, but its bearing on the question of mind in the *Amœba* is so obscure that we need not consider it further, but may pass at once to the study of the animal's reactions to special stimulation.

These are, according to Jennings (507, 512), the foremost authority on the behavior of the lowest organisms, three in number; namely, the negative, the positive, and the food-taking reactions. First, if an *Amœba* comes into strong contact with a solid obstacle in its movements, or if a solution of different composition from the water in which it lives strikes against it, or if one side of it is heated, the animal responds by contracting the part stimulated, releasing it from the substratum, and moving in another direction, usually one forming only a small angle with the preceding one. If the whole of one side or end receives a strong stimulus, if light falls on one side, or an electric current is passed through the water, the side stimulated—in the case of the electric current, the side toward the positive pole—contracts as a whole, and the movement takes place in the opposite direction. These phenomena constitute the *negative reaction* (Fig. 1).

Secondly, the reaction to solid bodies sometimes takes a *positive* form. In this case a pseudopodium is pushed forward in the direction of the stimulus, and the animal moves toward the solid. As the negative reaction serves the purpose of avoiding obstacles, so the positive reaction is useful in securing contact with a support on which to creep, and with food. It seems to be given in response to weak mechanical stimuli,

phenomena
 negative
 reaction

stronger ones producing the negative reaction. No chemicals have been found to occasion it, but weak chemical stimulation very likely coöperates with mechanical stimulation when the positive reaction is given to food. *positive reaction*

Schaeffer (898) has recently obtained evidence that *Amœba* can give the positive reaction to insoluble and inedible objects before they come into contact with it. The way in which such objects can act as stimuli is still unexplained. It is possible that the movement of the *Amœba* produces water currents which are reflected back in a peculiar way by such particles. He reports also (898) that the positive reaction is given to beams of light which pass no nearer than 100-150 thousandths of a mm. to the animal. The *Amœba* moves towards the beam, but when it comes into contact with it, the movement ceases, and in some cases a negative response occurs.



FIG. 1.—Negative reaction of *Amœba* to stimulation by a glass rod. *a.* Application of the stimulus. *b.* Change of direction of movement. After Jennings (512).

Thirdly, there is the *food-taking reaction*. This consists for *Amœba proteus*, according to Jennings, in the pushing forward of a pseudopodium on either side of the particle of food that has come into contact with the animal; the bending over of the ends of the pseudopodia so as to grasp the food, while "a thin sheet of protoplasm" spreads from the upper surface of the animal over it; and the final fusion of the ends of the pseudopodia and the ends of this sheet, so as to take the food directly into the animal's body. The reaction may occur anywhere on the body surface, there being no specialized mouth. It appears to be made only in response to edible substances, hence there is doubtless some chemical peculiarity about the stimulus which makes it effective (512). *food-taking reaction*

Kepner and Taliaferro (536) find the food-taking reaction more complex and variable than Jennings's account describes it to be. They observed cases where only one pseudopodium was formed, and cases where it was put forth not at the exact point acted upon by the stimulus. The nature of the reaction varied in such a way as to prevent the "swallowing" of too much water along with the food: "the parts that could most advantageously respond did so." McClendon (621) has at-



FIG. 2.—Food-taking reaction of *Amoeba*. 1, 2, 3, 4, successive stages. After Jennings (512).

tempted to apply the surface tension theory to the positive, negative, and feeding reactions of *Amoeba*, suggesting that the stimuli may exert an electric influence whereby the surface tension at the point stimulated becomes less in the case of the positive reactions and feeding, greater in the negative reaction. But such variations as those just described are difficult to reconcile with a surface tension theory. Moreover Mast and Root (663) have observed *Amoeba* crushing its prey with a force far greater than surface tension could account for. Schaeffer (897) suggests that a chemical discrimination may occur inside the *Amoeba* after substances have been taken in, for, he says, when carmine grains have been swallowed, the *Amoeba* at once begins to move off in such a way as to bring the grains to the hinder part of the body where they will be

ejected. "The carmine grains are ejected . . . because they are actually disagreeable and not merely because they are (presumably) indigestible." A hungry Amœba, when it comes within 100 thousandths of an inch from an organism, which is as a whole at rest but moving certain portions of its body, will begin to move towards it and to form a food cup before actual contact occurs. Probably the slight water currents produced by the movements of the prey act as the stimulus in this case. Any stimulus which proceeds from a moving object tends, as we shall see, to be peculiarly effective.

Kepner and Whitlock (538) report "that when Amœba encounters prey which is moving and hence likely to escape, it takes it in a wide embrace," so as not to disturb it prematurely: quiet prey is on the other hand "tightly surrounded." And they note that if the prey is an object which usually moves in a horizontal plane, the Amœba surrounds it in this plane first, and then cuts off vertical paths of escape.

- The positive and negative reactions, and the food-taking response with its modifications, make up, together with the ordinary crawling locomotion, the variety of the Amœba's experience as displayed in behavior, with the addition of a peculiar set of movements occurring in the absence of all mechanical stimulation. When an Amœba is floating in the water, through some chance, unattached to any solid, "such a condition," says Jennings, "is most unfavorable for its normal activities; it cannot move from place to place, and has no opportunity to obtain food." Its mode of getting out of the difficulty is to send out "long, slender pseudopodia in all directions," until "the body may become reduced to little more than a meeting point for these pseudopodia" (512, p. 8). As soon as one of these "feelers" comes in contact with a solid, it attaches itself, and the whole animal following soon takes up its normal crawling locomotion.

§ 9. *The Mind of Amœba*

Now what light does the behavior of Amœba throw upon the nature of the animal's possible consciousness? The first thought which strikes us in this connection is that *the number of different sensations occurring in an Amœba's mind, if it has one, is very much smaller than the number forming the constituent elements of our own experience.* We human beings have the power to discriminate several thousand different qualities of color, brightness, tone, noise, temperature, pressure, pain, smell, taste, and other sensation classes. Thus the content of our consciousness is capable of a great deal of variety. It is hard to see how more than three or four qualitatively different processes can enter into the conscious experience of an Amœba. The negative reaction is given to all forms of strong stimulation alike, with the single exception of food. We shall in the following chapter discuss more fully the nature of the evidence that helps us to conjecture the existence of different sensation qualities in an animal's mind; but it is clear that where an animal so simple in its structure as the Amœba makes no difference in its reactions to various stimuli, there can be no reason for supposing that if it is conscious, it is aware of them as different. The reaction to edible substances, is, however, unlike that to other stimulations. The peculiarity of edible substances which occasions this difference must be a chemical one. In our own case, the classes of sensation which result from the chemical peculiarities of food substances are smell and taste; evidently to a water-dwelling animal smell and taste would be practically indistinguishable. We may say, then, that supposing consciousness to exist in so primitive an animal as the Amœba, we have evidence for the appearance in it of a specific sensation quality representing the chemical or food sense, and standing for the whole class of sensations resulting from our own organs of smell and taste. The significance of the positive reaction is harder to determine. It seems to be given in response not to a special kind of stimulus, but

to a mechanical or food stimulus of slight intensity. In our own experience, we do not have stimuli of different intensity producing sensations of different quality, except in the cases of temperature and visual sensations. We do, however, find that varying strength of the stimulus will produce different *affective* qualities; it is a familiar fact that moderate intensities of stimulation in the human organism are accompanied by pleasantness, and stronger intensities by unpleasantness. The motor effects of pleasantness and unpleasantness in ourselves are opposite to each other in character. Pleasantness produces a tonic and expansive effect on the body, unpleasantness a depressive and contractive effect. In the *Amœba*, the positive and negative reactions seem to be opposed. The essential feature of the negative reaction is the checking of movement at the point stimulated; that of the positive reaction is the reaching out of the point stimulated in the direction of the stimulus. This much evidence there is for saying that besides a possible food sensation, the *Amœba* may have some dim awareness of affective qualities corresponding to pleasantness and unpleasantness in ourselves. It should, however, be borne in mind that wide differences must go along with the correspondence. In us, pleasantness brings a thrill, a "bodily resonance," due to its tonic effect upon the circulation, breathing, and muscles; unpleasantness has also its accompaniment of vague organic sensation, without which we can hardly conceive what it would be like. In an *Amœba*, it is clear that this aspect, as found in human consciousness, must be wholly lacking. Again, in the human mind pleasantness and unpleasantness are connected with various sensation qualities or complexes; we are pleased or displeased usually "at" something definite. The vagueness of the affective qualities in an *Amœba's* consciousness can only be remotely suggested by our own vague, diffused sense of bodily well-being or ill-being; and this is undoubtedly given its coloring in our case by the structure and functioning of our internal organs.

As for the peculiar behavior of an *Amœba* suspended in the

water and deprived of solid support, the stimulus for this must lie within the cell body itself. If any consciousness accompanies it, then the nearest human analogy to such consciousness is to be found in organic sensations, and these, as has just been said, must necessarily be in the human mind wholly different in quality from anything to be found in an animal whose structure is as simple as the Amœba's.

A consequence of this lack of qualitative variety in the sense experiences of an Amœba is a lack of what we may call complexity of structure in that experience. The number of stimulus differences which are in the human mind represented by differences in the quality of sensations is so great that at any given moment our consciousness of the external world is analyzable into a large number of qualitatively different sensations. At the present instant the reader's consciousness "contains," apart from the revived effects of previous stimulation, many distinguishable sensation elements, visual, auditory, tactile, organic, and so on. The Amœba's consciousness, if it possesses one, must have a structure inconceivably simpler than that of any moment of our own experience.

A second point in which the mind of an Amœba must, if it exists, differ from that of a human being, consists in its entire lack of mental imagery of any sort. Not only has the Amœba but three or four qualitatively different elements in its experience, but none of these qualities can be remembered or revived in the absence of external stimulation. How may we be sure of this? If our primitive animal could revive its experiences in the form of memory images, it would give some evidence of the influence of memory in its behavior. Indeed, as we shall learn, it is possible, in all probability, for an animal's conduct to be influenced by its past experience even though the animal be incapable of reviving that experience in the form of a memory image. Therefore, if we find no evidence that the Amœba learns, or modifies its behavior as the result of past stimulation, we may conclude a fortiori that it does not have memory images.

Now it would be stating the case too strongly to say that past stimulation does not affect the behavior of *Amœba* at all. In the first place, this animal shows, in common with all other animals, the power of "getting used" to certain forms of stimulation, so that on long continuance they cease to provoke reaction. "Thus," Jennings says, "*Amœbæ* react negatively to tap water or to water from a foreign culture, but after transference to such water they behave normally" (512, p. 20). Such cessation of reaction occurs when the continued stimulus is not harmful. In a sense, it may be called an effect of experience; but there is clearly no reason for supposing that it involves the revival of experience in the form of an idea or image. We have parallel phenomena in our own mental life. A continued stimulus ceases to be "noticed," but the process involves rather the disappearance of consciousness than the appearance of a memory image. Jennings, however, is inclined to think that preceding stimulation may modify the *Amœba*'s behavior in a way more nearly suggesting memory in a higher type of mind. He describes an interesting observation to illustrate this. A large *Amœba*, *c*, had swallowed a smaller one, *b*, but had left a small canal open, through which the swallowed one made efforts to escape, which were several times foiled by movements on the part of the large *Amœba* toward surrounding it again. Finally it succeeded in getting completely out, whereupon the large *Amœba* "reversed its course, overtook *b*, engulfed it completely again, and started away." The small *Amœba* contracted into a ball and remained quiet until through the movements of the large one there chanced to be but a thin layer of protoplasm covering it. This it rapidly pushed through, escaped completely, and was not pursued by the large *Amœba* (512, pp. 17-18), (Fig. 3).

Of this performance Jennings says: "It is difficult to conceive each phase of action of the pursuer to be completely determined by a simple present stimulus. For example . . . after *Amœba b* has escaped completely and is quite separate from *Amœba c*, the latter reverses its course and recaptures *b*."

What determines the behavior of *c* at this point? If we can imagine all the external physical and chemical conditions to remain the same, with the two Amœbæ in the same relative positions, but suppose at the same time that Amœba *c* has never had the experience of possessing *b*,—would its action be the same? Would it reverse its movement, take in *b*, then return on its former course? One who sees the behavior as it occurs can hardly resist the conviction that the action at this point is partly determined by the change in *c* due to the former possession of *b*, so that the behavior is not purely reflex" (512, p. 24).

If it is true that an Amœba which had not just "had the experience of possessing *b*" would not have reversed its movement and gone after *b* when the latter escaped, still we cannot think it possible that *c*'s movements in so doing were guided by a memory image of *b*. It may be supposed that the recent stimulation of contact with *b* had left a part of *c*'s protoplasm in a condition of heightened excitability, so that the weak stimulus offered perhaps by slight water disturbances due to *b*'s movements after escaping produced a positive reaction, although under other circumstances no reaction would have been possible. (Compare the observation of Schaeffer, just quoted, on Amœba's ability to react to objects not in contact with it). Mast and Pusch (663) have reported a possible case of learning in Amœba. As we have seen, when this animal comes in "contact" with a beam of light it gives the negative reaction. The experimenters found that it would then push forward again in the same direction, again encounter the beam, and withdraw. This proceeding would be repeated several times, after which the Amœba would change its path entirely. In the case of three of the five animals observed, the number of forward movements preceding the change of direction diminished in successive trials, separated usually by three-minute intervals. This type of modification in behavior will be discussed later (see Chap. X): it is not rapid enough to give evidence of the revival of memory ideas.

Let us consider for a moment some of the results of the absence of this kind of material in the possible mental processes of Amœba. In the first place, such a lack profoundly affects the character of the experiences which the animal might be supposed to receive through external stimulation. If we call the possible conscious effect of a mechanical stimulus upon the Amœba a touch sensation, the term suggests, naturally, such sensations as we ourselves experience them. In normal human beings touch sensations are accompanied by visual suggestions, more or less clear, of course, according to the visualizing powers of the individual, but always present in some degree. Fancy, for example, one of us entering a room in the dark and groping about among the furniture. How constantly visual associations are brought into play! Not once is a mere touch impression apprehended without being translated into visual terms; the forms and positions of the articles encountered are thought of immediately as they would appear if the room were lighted. The difficulty we have in thinking of a touch sensation with no visual associations illustrates the difference between our sense experience and that of an animal incapable of recalling images of past sensations.

It is equally obvious that in the absence of memory ideas, not only must the Amœba lack processes of imagination and reasoning, but there can be nothing like the continuous self-consciousness of a human being, the "sense" of personal identity, which depends upon the power to revive past experiences. It is even possible that the "stream of consciousness" for an Amœba may not be a continuous stream at all. Since its sensitiveness to changes in its environment is less developed than that of a human being, and there are no trains of ideas to fill up possible intervals between the occurrences of outside stimulation, the Amœba's conscious experience may be rather a series of "flashes" than a steady stream. And for the Amœba, again, we must remember that even such a series would not exist as such; the perception of a series would involve the revival of its past members. Each moment



Fig. 3.—Pursuit, capture, and ingestion of one Amoeba by another; escape of the captured Amoeba and its recapture; final escape. *b*, the captured Amoeba, was originally a fragment of another, *a*. After Jennings (512).

of consciousness is as if there were no world beyond, before, and after it.

Another consequence of that simplicity of structure which results both from the rudimentary powers of sensory discrimination and from the absence of memory ideas in the Amoeba's mind is that there can be no distinction, within a given mental process, between that which is attended to and that which is not attended to, between the focus and the margin of consciousness. Given a consciousness which at a certain moment is composed of the qualitatively different elements *A*, *B*, *C*, and *D*, we can understand what is meant by saying that *A* is attended to, is in the foreground of attention, while *B*, *C*, and *D* remain in the background. But given, on the other hand, a creature whose conscious content at a certain time consists wholly of the qualitatively simple experience *A*, it is evident that attention and inattention are meaningless terms. Different moments of its consciousness may differ in intensity; but attention, involving, as it does, clearness rather than intensity, arises only when mental states have become complex and possess detail and variety within their structure.

CHAPTER IV

DISCRIMINATION: METHODS OF INVESTIGATING IT

§ 10. *Preliminary Considerations*

WE have seen that the consciousness of an animal low in the scale contains few details, as compared with that of a higher animal. It is obvious that growth in the complexity of consciousness will occur by way of analysis. The more highly organized animal will be aware of complexities in its environment that wholly escape the more primitive mind. Further, we can see that an animal's ability to distinguish different features in its surroundings will rest upon several conditions.

The first of these is the nature of its sense-organs. If an eye lacks materials that can be affected differently by different colors, the corresponding color sensations will not appear in the mind of its possessor; if an ear has no apparatus for analyzing complex sound-waves, its possessor will be tone-deaf. A second condition for analyzing one's surroundings into various components is the ability to make different movements in response to different stimuli. If an animal under no circumstances could make different movements when acted upon by red and by green light; if he must invariably behave towards red as if it were green, and vice versa, we may venture the statement that he would not be aware of red and green as different. A full discussion of this statement would lead us too far into psychological theory. But in order to determine whether a particular type of animal is capable of distinguishing between two features of its environment, it is clear that we can appeal to two lines of evidence: that from structure of the sense-organs, and that from behavior.

§ 11. *Sense-organ Structure as Evidence of Discrimination*

The argument from structure is based on the fact that an animal has sense-organs recognizably like our own. If a creature has an organ suggesting strongly the construction of the human cochlea, or one with a lens and a membrane composed of rods and cones, it is highly probable that auditory stimuli in the one case and light in the other produce specific sensations. The usefulness of this argument is, however, limited in two ways. First, it is only a small part of the animal world whose sense-organs resemble ours closely enough to make the analogy safe. And secondly, we do not after all know very much about the relation of our own sense-organ structure to function. We know, for example, that our own organ with a lens and retina gives us visual sensations, and there is constantly accumulating evidence that the retinal rods mediate colorless sensations and the cones both color and colorless sensations; but we do not know anything about the retinal structures which underlie different qualities of color sensations. We can say that sensations of hearing come from the ear, but no one can tell us how to judge from the structure of the ear what range and fineness of pitch discriminations exist in its possessor's mind. No investigator has yet succeeded in relating the different qualities of smell and taste to differences in the end organs.

§ 12. *Behavior as Evidence of Discrimination*

The argument from behavior is as follows: If an animal reacts in a different way to two qualitatively unlike stimuli, then it may be supposed to receive qualitatively unlike sensations from them. If it always reacts in the same way to both, then both may be supposed to be accompanied by the same sensation quality.

But before conclusions can be drawn from this evidence, a third condition, besides sense-organ structure and capacity for

differential reaction, must be taken into account. An animal may fail to make certain movements not because they are in general impossible to it, but because it is already making other movements which are incompatible with the ones in question. For example, the general organic and motor disturbances accompanying fright are incompatible with those movements indicating discrimination. If an animal is not hungry, its tendency to make movements such as those of general exploration or play, or to assume the relaxation of sleep, may inhibit the movements of discriminating stimuli connected with food. In all experiments on animals, whether to determine their discriminative ability or their learning capacity, the first requisite is to furnish a *motive*. That is, the experiment must be so arranged that no tendency to move which would be incompatible with the one we wish to observe shall enter into competition with it; that some already strong tendency to move, whether inborn or acquired by experience, shall be brought to our aid.

Failure to observe this precaution destroyed the value of a method of experimentation formerly a good deal used, which may be called the Preference Method of testing discrimination. Vitus Graber, for instance, tried to find whether animals belonging to a variety of species could discriminate colors, by offering them the choice of two compartments, each illuminated by a different color. Clearly, if an animal chose one compartment as often as the other, it would be rash to conclude that the two lights produced for it indistinguishable sensation qualities. There might simply be the absence of any preference, along with perfect *capacity* for discrimination.

This consideration is the more important, the higher the animal stands in the scale. The higher animals have what might be called a large reserve fund of discriminations. That is, they are capable of making many more selective reactions to stimuli than they need at a given moment actually to use. Hence in their case the experimenter must make a careful adjustment of conditions to bring out exactly the discrimination

wanted. He must either make the performance of the reaction pleasant or its non-performance unpleasant to the animal. A monkey, for example, confronted by a set of glass tumblers covered each with a differently colored paper, may behave toward them all in precisely the same way; yet if food be put regularly in the blue tumbler, whose position in the row is varied, it becomes worth the monkey's while to make use of his discriminative powers, and he may show by his different behavior toward the blue tumbler that it produces on him a different impression from the others.

With simpler animals the problem is less difficult. If an animal is capable only of a half dozen different ways of responding to stimulation, we may with comparative safety assume that it has less opportunity to hold them in reserve; and if such an animal invariably reacts in the same way to two different forms of stimulus, or if the variations in its response are not correlated with differences in the stimulation, it becomes probable that the two stimuli produce in its assumed consciousness identical sensation qualities. Thus it is not the number of stimuli to which an animal reacts that can be taken as evidence of the qualitative variety of its sensations, but the number of stimuli to which it gives different reactions. When Jennings, for instance, says that *Amœba* "reacts to all classes of stimuli to which higher animals react" (512, p. 19), we cannot conclude that it possesses all classes of sensations that higher animals possess, for its reactions to these different stimuli are but little varied according to the kind of stimulus.¹

It should also, of course, be remembered not only that a motive must be supplied, but that the general physiological condition of the animal will influence behavior; a factor to which especial attention has been called by Jennings (512).

Obviously, in all experiments where behavior alone is the basis of inference regarding sensory discrimination, we must

¹ One of many reasons for the unsatisfactoriness of an article by A. Olzelt-Newin, entitled "*Beobachtungen über das Leben der Protozoen*" (731), lies in the author's uncritical acceptance of the hypothesis that reaction to a special kind of stimulus means a special kind of sensation.

make sure that the animal is really reacting to the stimuli whose effect we wish to investigate, and not to some other feature of the environment. Thus a dog in the Harvard laboratory was apparently discriminating accurately between two lighted areas of different size, but events proved that he was actually responding to slight pulls given by the experimenter on the leash that held him. He failed wholly when he was taken off the leash. Nowadays the careful experimenter always remains out of sight and hearing of the animal tested, and is not in contact with it in any way.

An ingenious way of getting evidence from behavior is the salivary reflex method devised by the Russian physiologist Pawlow (1122). The salivary ducts of the dog, which lie near the surface, are operated on so that the saliva can be discharged into a graduated tube. As is well known, the sight or smell of food increases the flow of saliva. Now when any other stimulus, such as a sound, regularly accompanies the sight or smell of food, this stimulus, originally without effect on the salivary flow, comes to increase the flow even in the absence of food. If, now, the stimulus that has thus acquired the power to affect the salivary flow is given in irregular alternation with another stimulus differing slightly from it, and the other stimulus is found not to affect the flow of saliva, then the inference can be drawn that sensory discrimination between these two stimuli is possible for the animal. It is maintained by some investigators that when sensory discrimination can be studied through such simple types of behavior as the salivary and other reflexes, there is less chance of misinterpretation than when more complicated choice processes are involved.

§ 13. *Evidence from Structure and Behavior Combined*

As a matter of fact, the argument from structure needs confirmatory evidence from behavior. For clearly the mere presence of a sense organ bearing sufficient likeness to our own to admit of conjecturing its function would be of no value as

proof unless it were shown that the sense organ actually functioned. In order to do this, it would be necessary to show that the animal reacted to the stimulus conjectured as appropriate to the sense organ, and that removal of the organ profoundly modified the reaction. Thus we shall find that many experiments to test sensory discrimination have been made by the method of extirpating a sense organ and studying the effect on behavior. The method has many disadvantages, the chief of which lies in the fact that it is hard to say which disturbances in behavior are due actually to the loss of the organ and which to the more widespread effects of the operation. Yet this much may be said for the combination of proof from structure and behavior involved in the Method of Extirpation, if we may so call it: where an animal reacts to a certain stimulus, for instance light, when a sense organ is intact, and fails to react to light, though otherwise normal, when the organ is removed, there arises a possibility that light may produce in the animal's consciousness a specific sensation quality, *even although the animal ordinarily reacts to light in a manner indistinguishable from that of its responses to other stimuli*. Though light and mechanical stimulation, for example, both ordinarily produce a negative reaction, yet if light brings about its effect only through the medium of a specialized structure with which mechanical stimuli are not concerned, then along with the probable unpleasantness accompanying the negative reaction there may go a quality peculiar to the functioning of that special structure.

Another mode of combining evidence from structure with evidence from behavior is by the use of localized stimuli. If an animal gives a response, which in itself may have nothing to mark it off from responses to other stimuli, when a special kind of stimulation is applied to certain regions of the body, and only then, while the other stimuli produce better reactions when applied elsewhere, then the suggestion is given that different sense organs are involved, and the same possibility arises of different sensation qualities.

Two other forms of evidence whereby from behavior a differentiation of sensory structures can be argued, and from differentiation of sensory structures possible differences of sensation quality, may be mentioned. The first of these consists in showing that reactions to different stimuli may be *independently fatigued*. The natural inference is that a specific nervous apparatus belongs to each stimulus. The second lies in demonstrating that the reactions to different stimuli occur with different degrees of rapidity. If there is a marked *difference in the reaction times* of an animal to different forms of stimulation, each, again, may be supposed to affect its own nervous pathway. A modification of this method consists in noting the influence of a stimulus upon the time of reaction to another nearly simultaneous stimulus. If such an influence can be shown, it is evident that the force producing it has some effect on the nervous system. By combining this method with that of extirpating a sensory structure, indications may be obtained that the nervous effect of the auxiliary stimulus is dependent on a definite receptive apparatus, and hence is probably accompanied by a special sensation. This method was used by Yerkes to demonstrate hearing in frogs (1104).

§ 14. *Evidence for Discrimination of Certain "Lower" Sensation Classes*

Bearing all these points in mind, let us proceed to survey the evidence for variety in the sensations of animals. In the lowest forms, such evidence must be derived entirely from behavior. That from the presence of a sense organ is almost wholly lacking. And although various stimuli, as we have seen, produce reactions in *Amœba*, yet there is only one case where these reactions are strikingly different according to the quality of the stimulus applied. This instance consists in the distinction between food-taking reactions, given to edible substances, and the responses to mechanical stimulation. The sense of touch, undoubtedly, must play a part in the mental life of the lowest

animals that have consciousness at all. But the earliest distinction between a touch quality and a quality that is other than touch seems to occur when food sensation and contact sensation are differentiated. It is possible that warmth and cold also appear as distinct sensation qualities in the experience of low forms of animals, but we have little real evidence of the fact. No organs of temperature sensation are definitely known even in human beings. And the responses of low animals to thermal stimulation are not specialized. They consist usually of negative reactions, or restlessness (412), when the animal is subjected to a temperature either above or below, but especially above, the "optimum"; and these reactions are not different from the ordinary negative type, suggesting unpleasantness rather than a specific sensation quality. In some cases the sensibility to thermal stimulation has been found to be differently distributed from that to other classes of stimuli. In certain insects the antennae probably test the air temperature, the tarsi that of the ground (412). But in any case, sensations of warmth and cold are probably in no member of the animal kingdom differentiated into any greater number of qualitatively distinct sensations.

The sense of touch, also, shows but little internal differentiation. Its importance, so far as we can judge, is rather on the spatial than on the qualitative side. The sense quality of pain we naturally think of as the accompaniment of the negative reaction in its more violent forms, given to a stimulus that is injuring the organism. Organic and kinæsthetic sensations are hard to trace in the lower animals; for animals whose structure differs widely from our own, the qualities of these two classes must remain beyond the power of our imagination. That differences in physiological condition such as are produced by hunger, satiety, or fatigue involve differences of accompanying organic sensation in the consciousness of the animal manifesting them is possible. Kinæsthetic sensations, as we shall see, are apparently concerned in the processes whereby many animals have learned to traverse a labyrinth path.

The three classes of sensation whose existence in the animal mind can be most satisfactorily traced are the chemical sense, under which smell and taste belong, the sense of hearing, and the sense of sight. To the study of these the following chapters will be devoted. Since the manifestations of the chemical sense in the lowest forms of animals consist chiefly in a differentiation of response to food and to mechanical stimulation, the contact sense or sense of touch will, in discussing these forms, be considered along with the chemical sense.

CHAPTER V

SENSORY DISCRIMINATION: THE CHEMICAL SENSE

A MAJORITY of the animals below the insects in the ascending scale of animal life dwell in the water. For these smell and taste are virtually the same; if they perceive food at a distance, it is because the food juices are diffused through the water. Lloyd Morgan (701) has proposed the term "telæsthetic taste" for the chemical sense of an aquatic animal, indicating that this sense corresponds to taste in an air-dwelling animal because its stimulus is fluid, but differs in that it allows perception of distant objects.

In the last chapter we saw that our first step, in trying to find out whether an animal discriminates between certain stimuli, is to ask whether its reactions to one stimulus differ from those to the other. Hence we shall have to note the cases in which lower invertebrates react to chemical stimuli in a manner unlike their behavior to other stimuli, for instance to contact. It will not always be easy to decide whether the stimulus is chemical or mechanical; whether an animal distinguishes food, for example, from other substances because it tastes different or because it feels different.

It appears that the functions of the chemical sense in lower invertebrates are, first, to enable them to distinguish what is good to eat from what is not, and secondly, to make them avoid harmful chemicals. This latter function, evidently, will be served by an ordinary negative reaction. If all that is necessary is to get away, the mode of departure need not be different whether the stimulus is chemical, or mechanical injury, or high temperature. And the conscious accompaniment may well

be the same in all cases. Food reactions will be more likely to furnish evidence of true sensory discrimination.

§ 15. *The Chemical Sense in Protozoa*

We have found that the most primitive type of protozoön, *Amœba*, reacts differently to edible and to inedible substances. While it will sometimes "swallow" inedible particles such as grains of carmine, it takes immediate measures to get rid of them, measures too prompt to be the result of an attempt at actual digestion, and hence properly to be regarded as the effect of a chemical or food sense. Many members of the lowest division of the animal kingdom, the single-celled Protozoa, have a structure decidedly more complicated than that of *Amœba*. There is a large group of them called Ciliata, from the fact that their bodies are covered with little hair-like protoplasmic filaments or cilia, which serve as organs of locomotion by acting like tiny oars. These animals have a definite bodily region for food-taking, which is surrounded with longer cilia beating with especial vigor and creating currents that sweep food particles in. A common representative of the Ciliata is *Paramecium*. Instead of crawling about, like *Amœba*, this animal swims freely and rapidly. Its needs are therefore well served by the very definite and vigorous negative reaction which gets it out of trouble. This is given when it swims against a mechanical obstacle, or into strong ultra-violet rays (411), or into temperatures above or below the optimum between 24° and 28° C. The reaction consists, according to Jennings, of the following process: the animal darts backward, reversing the beat of its cilia, turns toward the aboral side (that opposite to the mouth groove) by increasing the beat of the oral cilia and lessening the compensating rotation, and continues on a forward course that is now at an angle with its former line of motion. If this new course carries it clear of the stimulus, it continues on its way; if not, repeated contact with the stimulus causes a second reaction, the Para-

meccium always turning in the same direction, so that ultimately it avoids the source of stimulation (495, 512) (Fig. 4). Differing strengths of stimulus produce the reaction with different degrees of violence. Clearly this response, given alike to mechanical, thermal, and chemical stimulation, offers no evidence that chemical stimuli are discriminated from the others.

While *Paramecium* definitely avoids by the negative reaction certain chemicals introduced into the water, it shows a

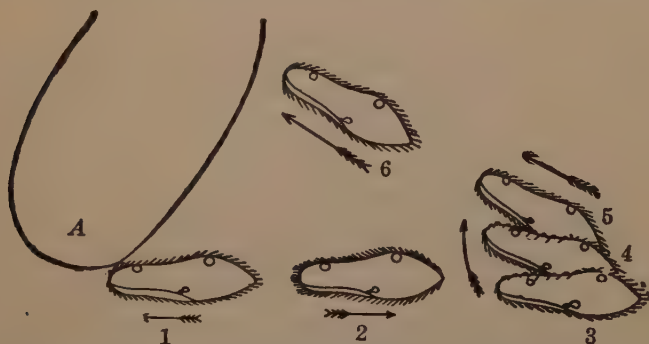


FIG. 4.—Negative reaction of *Paramecium*. A is the source of stimulation. 1-6 are the successive positions of the animal. After Jennings (512).

tendency to collect in the neighborhood of others. Such is the case with weak acids, with a bubble of oxygen if air has been long excluded from the slide, and with carbon dioxide, which in water of course produces acid (512). Jennings pointed out that the inclination of *Paramecium* to gather in groups is very likely due to the attraction for them of the carbon dioxide which they excrete. But he has also shown that this "attraction" to certain chemicals does not mean the presence of a special positive reaction. The fact is that when the animals collect in a drop of weak acid, for example, they are not attracted toward the acid. They simply happen, in their ordinary movements, to swim into it, and on entering it show no disturbance whatever. But when they come to the edge of the

locobog
"grouping"
persistent

drop on the way out, they give the negative reaction to the surrounding water. Thus they are, as it were, trapped within the drop.

The nearest semblance to a positive reaction in *Paramecium* is found in the fact that sometimes, when it comes into contact with a solid, instead of darting backward it merely stops and extending stiffly the cilia which touch the object, remains at rest (Fig. 5). This behavior is useful because around decaying vegetable matter, the kind of solid oftenest found in the animal's ordinary environment, there is apt to be a supply of food in the form of bacteria; it is a good anchorage. What characteristics of the stimulus determine that this contact reaction, or "thigmotaxis," rather than the negative response, shall be given? That it occurs when the mechanical stimulus is of low intensity is suggested by the fact that it is more likely to be made if the animal comes against the solid when swimming rather slowly. Perhaps also the spatial distribution of the stimulus over several points of the body increases the probability of a contact rather than an avoiding reaction. Jennings says that *Paramecium* tends to come to rest against loose or fibrous material, which gives contact at several bodily regions at once, rather than against smooth hard material such as glass (512).

All the free-swimming Protozoa react to chemicals in the water after the manner of their ordinary negative reactions, and we must examine their behavior to food if we want to find evidence of discrimination. Do they select edible particles from inedible ones? And if so, does the selection occur because of the chemical difference between food and not-food, or because of differences in mechanical properties, that is, in "feel"?

Most of the Ciliata whose behavior has been observed do, it appears, reject from the mouth region particles that are unsuitable for food, by reversing the direction in which the cilia surrounding this region are whirling. In some cases the observers claim that the basis of discrimination is chemical, in

other cases that it is mechanical, while in still others no evidence is forthcoming as to its nature. Jennings (512) reports no rejection of unsuitable particles by *Paramecium*, but Metalnikow (675, 676) says that when *Paramecia* have been kept for some time in water containing carmine grains they cease to swallow them; the evidence being that fewer and fewer grains are found in the animals. Schaeffer (895) thinks this result is due to the mechanical change in carmine grains that have been long in the water, which become stuck together in the mucus excreted by the *Paramecia*. Metalnikow (677) however finds that when fresh carmine is used the *Paramecia* avoid it apparently as a result of their previous surfeit, and that when particles of aluminum are used instead of carmine they acquire a discrimination against these even more quickly. He therefore feels convinced that the discrimination is a chemical one.

Stentor is a ciliate protozoön which spends a part of its existence anchored by a long extension of its body, like the stem of a flower: at times it pulls this up and swims off. Food is taken in by the whirl of cilia around the mouth, and may be rejected by a reversal of the direction of this whirl. Schaeffer (895) says that *Stentor* discriminates not only between organisms and inedible particles, but between different kinds of organisms; he thinks, however, that the basis of discrimination is not chemical, because food soaked in a variety of chemicals is readily taken, while jelly made of food organisms is rejected. He believes the discrimination rests probably on several mechanical factors in combination, for example, size, weight, form, and surface texture, no one of which is alone sufficient to determine the choice. On the other hand Lund (615), observing another ciliate named *Bursaria*, finds that this organism will reject yolk of egg particles if they have been treated with certain dyes,



FIG. 5.—
Positive
thigmotaxis
in *Paramecium*. After
Jennings
(512)

and concludes that the basis of discrimination is chemical. *Lacrymaria*, another ciliate, tests with its "head" objects within reach and rejects the inedible, on what basis we have no information (649). *Didinium* is a ciliate which has a peculiarly modified seizing organ, but the only selection of food which it makes rests on the fact that this organ will adhere to the surfaces of some organisms and not to that of others (646). Two other protozoa, *Actinobolus* and *Spathidium*, have each so far refined the process of food selection that they swallow only one kind of organism. *Actinobolus*, an anchored form, awaits its destined prey, and *Spathidium* selects it in freely swimming about, but whether the prey is recognized by the chemical sense or by touch we do not know (693).

In general, it may be said that some Protozoa give evidence of a true chemical sense in distinguishing their food from other substances by virtue of its chemical properties.

§ 16. *The Chemical Sense in Cœlenterates*

In the cœlenterates, the most important group of animals standing just above the Protozoa, the general plan of bodily structure is that of a hollow sac, whose walls consist of two layers of cells, food being taken into a mouth at one end of the sac, and the arrangement of the cells being on the plan of circular symmetry. In this class are included sea-anemones, jellyfish, the little green or yellow *Hydra*, and corals.

Some cœlenterates give to food substances a response *differing in kind* from that which they make to inedible substances. This is true of *Hydra* (Fig. 6), which seizes food with its tentacles, but withdraws them and contracts on its stem if touched by anything else. The food stimulus seems to be both chemical and mechanical, such as is offered by contact with a solid edible object (1024). Whether the conscious aspect of such a reaction corresponds to a food sensation or to vague pleasantness is uncertain, for the food-taking response is the

only form of the positive reaction in *Hydra*. Special food responses occur in many sea-anemones. W. H. Pollock a number of years ago reported his observation that certain unnamed sea-anemones opened out if food were suspended near them in the water, and referred the phenomenon to "a sense of smell" (827). *Adamsia rondeleti* winds its tentacles around bits of sardine meat and passes them from tentacle to tentacle toward the mouth. When balls of filter paper softened with sea water are substituted, the feeding reaction is wholly lacking. Either the tentacles fail to react at all, or the ball is "felt of" slowly with no attempt to seize it, or it is momentarily seized and then dropped. If the paper ball be soaked in fish juice, on the other hand, it is seized as eagerly as the fish meat. A negative reaction, consisting in the withdrawal of the tentacles affected, may be produced by applying a bit of paper soaked in quinine solution or by the discharge of quinine solution from a pipette near the tentacles (593, 718). A

peculiar form of negative reaction has been observed in *Adamsia*, and more strikingly in *Cerianthus*, when a paper ball soaked in fish juice has been passed from tentacle to tentacle till it has nearly reached the mouth. The process is suddenly reversed, and the ball is passed back from one tentacle to another till it reaches the outside edge and is dropped off. Nagel, the observer, thinks the stim-



FIG. 6.—*Hydra*. *mth*, mouth; *t*, tentacle. After Parker.

ulus for this change of reaction is the gradual wearing off of the "sapid parts" of the ball during its passage toward the mouth—it might be the squeezing out of the meat juice—and calls special attention to the fact that the reaction whereby the paper is got rid of is wholly different from the ordinary reaction of a tentacle to mechanical stimulation, which, as we have seen, does not involve seizing the object at all. A tentacle touched by a bit of moistened filter paper ordinarily responds, if at all, by a mere contraction without the winding seizure of



FIG. 7.—*Metridium*. After Parker.

the object. Touched by the same object "handed on" to it by a tentacle nearer the mouth than itself, it seizes the paper and passes it on to the tentacle beyond it. The cause of this difference in behavior seems to lie in the processes that have been taking place just previously. Nagel does not hesitate to say that a psychic process must be involved, but its details are not easy to construct (721).

Metridium (Fig. 7), the common pinkish brown sea-anemone of our North Atlantic coasts, has a definite response made to food and nothing else, but no special rejecting response for inedible substances. If dropped on a tentacle, the latter are carried by the ordinary waving motion of the cilia which goes on all the time, to the tentacle tip and dropped off. But when a bit of crab meat, for instance, is put on a tentacle, the latter contracts and curls over with the tip directed towards the mouth; the ciliary motion continuing in its usual direction now of course carries the food to the mouth. If the food is applied to the lips on either side of the mouth, the response is different: the cilia here reverse their motion and thus pass it into the mouth (739).

Some jellyfish also make special reactions to food stimuli; the little *Gonionemus* (Fig. 8), for instance, also common in the Atlantic. The body of a typical jellyfish or medusa con-

sists of a bell-shaped "umbrella" from the edge of which tentacles depend. Hanging from the middle like the clapper of the bell or the handle of the umbrella is the manubrium, at the end of which is the mouth. If *Gonionemus* is touched by an inedible object it swims away, by contractions of the bell which start at the point touched; if it is touched by food, the tentacles twist round the food, bend towards the manubrium, carrying with them the margin of the bell, and the manubrium swings over and swallows the food (1095). It is an interesting fact that if the inedible stimulus *moves*, as when a glass rod is drawn across the tentacles, the beginning of the food response is made. Special reactions to moving stimuli are widespread throughout the animal



FIG. 8.—*Gonionemus*. After Hargitt.

kingdom; their significance will be discussed in Chapter VIII.

Other coelenterate animals give evidence of a special food sense not by a special kind of reaction to food, but merely by a *more intense and vigorous reaction* than they give to inedible materials. For instance, in *Tubularia*, which belongs to the family of hydroids, forming colonies of many individuals on a common stem, when a grain of sand was put in contact with the tentacles on one side and a bit of meat on the opposite side, the reaction was almost invariably in the direction of the meat. Filtered meat juice allowed to flow on the tentacles produced a reaction 82 percent. of the time, while carmine water was effective only 15 percent. of the time (776). The sea-anemone *Aiptasia* reacts to both contact stimulation and to contact plus food stimulation by winding the tentacles around the object and directing them toward the mouth, but the reaction to food is more vigorous (721). One species does react differently to plain filter paper and to filter paper soaked in crab juice

(508). Another sea-anemone is so indifferent to chemical stimulation that it will take filter-paper soaked in acetic acid (304). In the jellyfish *Carmarina* there is no difference between the reaction to contact and that to food, except that the latter is more prompt (719, 721).

We saw in Chapter IV that if the sensibility to two different kinds of stimuli is *located on different parts of the body*, we may infer that the two are discriminated even though the responsive movements are the same. This is the case with *Carmarina*. The skin of the under side of the umbrella and that of the manubrium are very sensitive to mechanical stimulation and not at all so to chemicals, while the tentacles respond more readily to chemical than to mechanical stimuli (719, 721). The ctenophore *Beroe ovata* is sensitive to irritating chemicals (food stimuli were not tried) only around the edges of its mouth, while the opposite end of the body is highly responsive to touch. This animal rises to the surface of the water upside down and turns over to the mouth-side up position; Nagel (719, 721), who studied it, thinks the sensibility of the aboral end causes the turning over, the change from water to air pressure acting as the stimulus. The location of chemical sensibility in sea-anemones varies in different species (721, 593, 304).

The effect of an animal's *physiological condition* on its reactions to food is marked among many coelenterates. If *Hydra* is very hungry, its food response, which is normally given only to food, will be produced by any chemical stimulus, even quinine (1024). This blunting of discrimination has, of course, the adaptive aspect that the starved animal can afford to lose no chances, and suggests the analogy from our own experience of the loss of intellectual discrimination in moments of intense emotion. For the emotion represents a situation where the organism cannot afford to lose chances by hesitating in reaction long enough for nice discrimination. Certain sea-anemones, for instance *Adamsia* (721) and *Sagartia* (976) also swallow inedible substances if hungry enough. *Stoiachactis*

will give a negative reaction to food if it is not hungry (508); Metridium on the other hand will take food as long as it has room for it, though not so promptly as when hungry (512).

In all coelenterates whose behavior has been observed, it thus appears, there is evidence of a specialized food sense; either the animals give a special type of reaction to food, or a specially rapid or vigorous reaction, or a reaction when the stimulus falls on a special region of the body.

A certain amount of discrimination among mechanical stimuli is ascribed to sea-anemones by Romanes. "I have observed," he says, "that if a sea-anemone is placed in an aquarium tank and allowed to fasten upon one side of the tank near the surface of the water, and if a jet of sea water is made to play continuously and forcibly upon the anemone from above, the result of course is that the animal becomes surrounded with a turmoil of water and air bubbles. Yet after a short time it becomes so accustomed to this turmoil that it will expand its tentacles in search of food, just as it does when placed in calm water" (874, p. 48), although the solid stimulus is decidedly less intense than that offered by the bubbles. Similarly, Fleure and Walton find that certain species show little reaction to accidental contact with a pebble that is moved, but react quickly to a finger (304).

§ 17. *The Chemical Sense in Flatworms*

Next to the coelenterates zoologists place the phylum of the flatworms, which possess a bilaterally instead of a radially symmetrical structure. Many representatives of the group are parasitic, and so far as the writer is aware, no one has studied their reactions to stimulation. Most of our knowledge in regard to the sensory life of the flatworms is confined to the common freshwater planarians, small slow-moving creatures which crawl on solid objects under water or on films covering the surface, and can usually be found on the under surface of decaying leaves in fresh water. The mouth is on

the ventral side of the body, sometimes quite far from the head end (Fig. 9).

Planaria maculata gives a positive reaction, that is, turns its head and moves towards food, but it does the same towards a



FIG. 9. — Planarian, dorsal view. After Woodworth.

weak mechanical stimulus (773). A planarian will follow an object such as the point of a pin moved in front of it, and one planarian will follow the trail of another that happens to come within the proper distance. Similarly, the neighborhood of food will cause the animal to turn toward it. Bardeen has suggested that the so-called "auricular appendages," two small movable prominences on the animal's back near the head end, which are specially sensitive to touch, may be "delicate organs capable of stimulation by slight currents in the water set up by the minute organisms that prey" upon the animal's food; so that the positive reaction when given to food may be really a response to mechanical stimulation (29). As Pearl, however, found that chemicals, diffused in the water, would produce positive responses (773), it is probable that *Planaria maculata* is directly sensitive to chemical stimulation, though it responds thereto in the same way as to mechanical stimulation. A land planarian, *Geodesimus bilineatus*, is reported by Lehnert to perceive food at distances from four to five times the

length of its body, and he does not describe the positive reaction as given in response to any other than food stimulation (582).

The actual feeding reaction of planarians does indicate a true chemical sense, as the positive reaction, being given in most cases alike to food and touch, does not. When an object which has attracted *Planaria maculata* into crawling toward it

is reached, the head folds over it and grips it, contracting so as to squeeze it. The substance being thus brought into contact with the mouth (pharynx) on the under side, swallowing movements are made if the proper stimulus is given. In *Microstoma*, the organ of the chemical sense has been held to be the sensory epithelium in the floor of the pharynx (536). Bardeen was inclined to think that contact with a soft substance constituted the proper stimulus, as he found that hard particles placed on the pharynx were not swallowed (29). Pearl, however, believes that mechanical and chemical stimulation must combine. The former alone does not suffice, for swallowing movements are not evoked when one planarian crawls over another; the latter alone is insufficient, for placing the animal in a sugar solution has no effect. If chemical and mechanical stimulation are united, the reaction is given whether the chemical is edible or not; Pearl found it occurring in response to sodium carbonate (773).

Planarians thus appear to distinguish chemical from touch stimuli, but not, so far as has been observed, foods from other chemicals. They give negative reactions to strong stimuli, either chemical or mechanical; the conscious accompaniment suggested by these would be mere unpleasantness, as that of the positive reaction is pleasantness.

Evidence of the influence of *physiological condition* on the reactions of planarians is furnished by the fact that the resting planarian is less sensitive. Bardeen found that if the animal was not in motion already, it gave no positive response to food in its neighborhood (29).

§ 18. *The Chemical Sense in Annelids*

Next above the planarians come the annelids or segmented worms, of which the earthworm is the most familiar example. Many other annelids are water-dwelling, and hence smell and taste are one to them. That earthworms distinguish edible from inedible substances in contact with the body,

Darwin thought probable from the apparent preference of the worms for certain kinds of food (229). In the earthworm *Allolobophora* touch and chemical stimuli are discriminated from each other. These worms live in barnyard manure. When placed on scraps of shredded filter paper moistened with water they refuse to burrow; when the filter paper is wet with a decoction of the manure they burrow as soon as they come into contact with it. The adequate stimulus for burrowing is thus a combined mechanical and chemical one; the chemical stimulus alone is insufficient, for filter paper thus prepared has no effect on the worms unless they are actually in contact with it (934). Using the human terms, the case is one of taste rather than smell. Nagel suggests that the earthworm's chief use for a chemical sense is to help it find the moisture which is necessary to its life (722); but curiously enough *Allolobophora fætida* seems to have no power of doing this from a distance. Smith found that a worm would crawl around a wet spot on paper until its skin dried, without crawling into it. If by accident it happened to touch the moist place, it would enter and remain there (934). Parker and Parshley (765) find that the head end of the worm is negatively stimulated by contact with a dry surface, and will withdraw soon after such contact. There seems no satisfactory evidence that worms respond to chemical stimulation from a distance by positive reactions, although Darwin believed that they found buried food by "the sense of smell" (229). Chemical stimuli not in contact with the body do produce negative reactions (722), but these reactions do not differ from the responses to strong mechanical stimulation. They are of various forms—turning aside, withdrawing into the burrow if the tail is already inserted, squirming, and so on, the differences being correlated with differences in the intensity and location of the stimulus and in the excitability (physiological condition) of the animal. But nothing in the character of the response suggests that negative reaction to a chemical stimulus has a different conscious accompaniment from that of negative response to a mechanical stimulus.

The most natural interpretation of them all on the psychic side is that of unpleasantness, increasing in intensity as the reaction takes a more violent form.¹ Leeches seem to be excited to their feeding reaction by a combination of mechanical and chemical stimulation. They are very sensitive to slight water disturbances, and react by stopping the respiratory movements if a needle is touched to the surface of the water above them. Food juice diffused through the water makes them very active; while in this state they will attach themselves to a glass rod, but drop off at once. When they attach themselves to food substance, however, they hold on with traditional tenacity. Chemicals of various kinds produce withdrawing reactions, and Löhner (605) finds evidence that leeches experience "taste compensation." When we have to eat sour fruit we cancel the sour sensation by putting sugar on the fruit. A five per cent sugar solution produced withdrawing reactions in a leech, but if the sugar solution was mixed with a nine per cent. salt solution, its strength had to be raised to seven and five-tenths per cent. before the leech reacted to it.

Kribs (562) has obtained evidence of *localized chemical sensibility* in the annelid *Aeolosoma*; weak chemicals will produce a reaction only if applied to the sensory hairs of the head end. The marine worm *Nereis* shows localized sensibility to chemicals on the palps and tentacles, although no sense cells have been found there, and little or no use is made of the chemical sense in finding food (369).

The *time occupied in reacting* has been made a basis for differentiating the response to different chemicals in earthworms. It was found that if the worms were suspended by threads, and

¹ W. W. Norman argued that the squirming reactions of worms, and the corresponding reactions of other animals to injurious stimulation, cannot be taken as evidence of an accompaniment of disagreeable consciousness, because of the fact that when the worm, for instance, is cut in two, the squirming movements are confined to the posterior piece, while the head end crawls away undisturbed. The head end, he urges, containing the cerebral ganglia, ought to be the part capable of suffering, but it gives no reaction (726). We cannot, however, conclude from the absence of a reaction under abnormal conditions that when it occurs in the normal state it has no conscious accompaniment.

their anterior ends dipped into solutions of sodium, ammonium, lithium, and potassium chlorides, the animals reacted to these substances with diminishing promptness in the order just given. The differences in reaction time were marked. Now all four of these substances produce in man nearly the same taste quality, salt, for which the common constituent chlorine is therefore held responsible. The sodium, lithium, ammonium, and potassium ions have apparently but little effect on the human taste organs. Since the earthworm reacts with decided time differences to the four, it may be that its taste organs are specifically affected by each, and that different taste qualities may be occasioned in its consciousness (764).

§ 19. *The Chemical Sense in Molluscs*

As for the molluscs, the headless ones or Acephala, such as the clam, oyster, and scallop, do not feed actively at all, but digest such food as the water currents sweep into their bodies; hence they have little use for a chemical sense. Some snails have been observed to have special responses to food. The fresh-water snail *Physa* shows an interesting relation between food and touch stimuli. "If *Physa*," says Dawson (239), "was moving at a moderately rapid rate when it came in contact with the meat, it received a sufficiently strong stimulus to cause it to turn away, to pause and then turn back. It would seem that the mechanical stimulus was not only sensed first but obeyed, and then the chemical stimulus was in turn sensed and obeyed." Copeland (194) has found that the marine snails *Alectrion* and *Buscyon* could distinguish from a distance a packet containing food from one containing cloth. The land snail *Helix* reacts positively to food and negatively to many chemicals before coming in contact with them (909).

In lamellibranchs, a division of the Acephala, sensibility to chemical stimuli seems pretty well distributed over the body surface, but in snails it is *localized*. Nagel (722) regarded the horn as the most sensitive region in marine snails; Piéron (801)

analyzes the situation further and finds in these snails three modes of chemical excitability; an aerial distance excitability, on all parts of the body with predominance of the mouth, the anterior edge of the foot, and the siphon; a contact sensibility in both air and water, on the mouth, the horns, and probably elsewhere; and a delicate distance sensibility in the water, located in the regions of the mouth, the horns, the anterior edge of the foot, and the osphradial region. Copeland's observations on his marine snails indicate that the apparatus for sensing distant food is the siphon, which has at its end a shifting "nostril" for sampling water; and that taste, the sense for food in contact with the body, has for its organs the horns, the front end of the foot, and the under part of the head (194). The land snail *Helix*, according to Yung, smells with the ends of its horns, although even when deprived of horns it can distinguish perfume; its sense of taste is best developed near the lips, and touch sensibility is distributed over the body, but especially toward the end of the horns (1127, 1128).

§ 20. *The Chemical Sense in Echinoderms*

In the phylum of the echinoderms, under which are classed starfish and sea-urchins, the "circular symmetry" of body structure characteristic of the coelenterates reappears. Starfish were found by Romanes many years ago to show, besides pronounced negative reactions to strong or injurious mechanical stimulation, what he called a sense of smell. Its manifestations depended on the *physiological condition* of the animal; that is, upon its degree of hunger. If kept several days without food, a starfish would immediately perceive its presence and crawl toward it. "Moreover, if a small piece of the food were held in a pair of forceps and gently withdrawn as the starfish approached it, the animal could be led about the floor of the tank in any direction." By cutting off various parts of the rays, Romanes found that "the olfactory sense

was equally distributed throughout their length"; and he also showed that the ventral and not the dorsal surface of the body was concerned, by varnishing the latter, which left the reactions unaffected, and by observing that when a bit of food was placed on the back it remained unnoticed (873, pp. 321-322). Preyer reported great individual differences in the responses of starfish to food stimulation; while certain specimens were unmoved by the neighborhood of food, an individual of another species came from more than six inches away and fell upon it (835). Whether the unlikeness of behavior was due to the species difference or to a difference in the degree of hunger does not appear. In the holothurian *Thyone briareus* feeding movements could not be produced by external stimuli, and apparently result from the internal state of hunger (777).

§ 21. *The Chemical Sense in Crustacea*

The highest invertebrate animals belong to the phylum of the Arthropoda, like the annelid worms in their segmented structure, but more highly organized in many respects. The body of a typical arthropod consists of a series of segments, one behind another, each segment with a pair of appendages. The higher an arthropod stands in the scale, the more modification and differentiation of function there is in the segments and appendages; the former often become consolidated, and the latter become modified for swimming, walking, or sensory purposes. The lowest grand division of the Arthropoda is that of the Crustacea.

As the animals of this group are covered with a hard outside shell, sensitiveness to touch and chemical stimulation is ordinarily referred to certain hairs scattered over the body, and to the modified appendages of the anterior segments which we commonly know as "feelers," the large and small antennæ. That mechanical contact stimuli in certain Crustacea give rise to specialized reactions is evidenced by observa-

tions on the hermit crab. This animal, as is well known, has acquired the instinct of taking up its abode in empty shells, most commonly those of some gasteropod mollusk. When wandering about in search of a dwelling, the crab's reactions to the objects it meets show adaptation to the character of the stimulus, for it will not investigate a glass tube or ball; the smooth surface seems not to be the adequate stimulus for beginning the movements involved in exploring and entering a shell (357).

The responses of Crustacea to food stimulation vary, as might be expected, with different genera and species. Nagel finds the rôle of the food sense in aquatic Crustacea very insignificant; they occasionally show antennal movements in the presence of food, he says, but are not guided to it (722). That general restlessness is shown by various Crustacea in the neighborhood of food, but not in contact with it, has been observed by Bell in the crayfish (49), by Holmes in the amphipod *Amphithoe longimana* (455), by Bateson in shrimps and prawns (33), and by Bethe in the green crab (59). Bethe arranged a series of aquaria one above the other, with a connection between them, and found that when food was placed in the uppermost compartment the crabs in the lower ones were successively excited as the food juices diffused themselves from each compartment to the one below. The crayfish's reactions to contact with food are such as to direct the stimulus toward the mouth; negative reactions of rubbing, scratching, and pulling at the affected part were obtained by stimulation with acids, salts, and other irritants (50). Chidester (166) found that the crayfish would go to freshly cut meat more quickly than to meat whose surface had had time to dry. Evidences of irritation in the neighborhood of asafœtida were observed by Graber in (363). The Dutch physiologist Buytendijk (148) has used on the little fresh water crustacean *Daphnia* an ingenious method for comparing the effectiveness as stimuli of different chemicals which can be derived from food. A single

Daphnia was placed in a round vessel on a dark ground, the bottom of the vessel being divided into quadrants. The movements of the animal were watched from above and a record of them traced; the time spent in each quadrant was also recorded. After it had been proved that the animal visited all quadrants equally, a stimulating substance was put into one quadrant. The records showed attraction to milk or a crumb of bread; also to the higher fatty acids and the lower alcohols; negative response to the lower fatty acids and higher alcohols. When two stimuli each in a different compartment were used, their influence could be compared: bread proved able to counteract the attraction of light within a certain range of intensities.

As regards the location of the chemical sense-organs, in *Amphithoe* the small antennæ (antennules) and the mouth parts seemed to be the regions especially sensitive to food stimulation; if the food touched one of the former, the animal instantly made a dart for it. Touching the antennule with a needle very rarely caused such a reaction (455). Bateson's shrimps and prawns had their food sensibility located chiefly in the antennules, though if food was placed very near them they would show disturbance even when deprived of antennules (33). Balss (24) finds the sense of smell in the shrimp *Palæmon* located in the antennæ, and also in other parts; taste in the mouth parts and tips of the thoracic legs. This was the case also with Holmes's amphipod. Bell, on the other hand, found the whole body of the crayfish sensitive to chemical stimulation, and no evidence that the small antennæ were especially concerned.

A new function for the chemical sense now makes its appearance. In some Crustacea the sense of smell is possibly concerned in guiding the male to the female. Certain copepods which daily migrate from near the surface of the water to greater depths and back again have had this behavior explained as a result of the reactions of the females to light, plus the tendency of the males to follow the females. That

the latter is an affair of chemical stimulation is indicated by the fact that the females were sought even when concealed in tubes (740). In the case of some other Crustacea, however, the sexes do not seem to be aware of each other's neighborhood until they come into actual contact (457, 459).

§ 22. *The Chemical Sense in Arachnids*

The two most important divisions of the arthropod group besides the Crustacea are the Arachnida, of which spiders and scorpions are typical examples, and the Insecta. Spiders, as is well known, have highly developed responses to touch stimulation; the web-making spiders in particular are sensitive to very slight web vibrations. The food reactions of spiders, so far as the writer knows, have never been studied from the point of view of the chemical sense (but see page 109). Various observers report sensitiveness to chemical stimulations, such as those produced by odorous oils, not in contact with the body. Spiders of the family Attidæ would react to glass rods dipped in such oils and brought close behind them, but would not react to clean glass rods when similarly placed (782). The reactions seem to be of a negative character (837), and, of course, in all such cases it remains uncertain whether the possible conscious accompaniment is a specifically olfactory unpleasantness or an unpleasant irritation of the body surface. Pritchett found that irritating and non-irritating oils produced negative reactions (837); but an oil that belongs, for us, to the latter class might belong to the former in the case of a spider. If the sensibility were sharply localized, that fact would point in the direction of a specific olfactory sensation; but while some authorities think the spider's feelers or palpi are smell organs (57), others believe that sensibility to chemical stimulation is distributed over the body (622, 837). Nagel finds no specific organ of smell and little smell sensibility in spiders (722).

A member of the Arachnida which presents but slight superficial resemblance to the spiders is *Limulus*, the horseshoe crab. *Limulus* shows taste reactions, but no response to smell stimuli. If the mandibles at the base of the legs be rubbed with inedible objects, there is no reaction. Similar negative results are obtained by holding strong-smelling food close to the mouth or jaws. But if an edible substance be rubbed on the mandibles, strong chewing movements take place. Ammonia or acid vapor will produce these same chewing reflexes, but the claws make snapping movements "as though to pick away some disagreeable object." If a wad of blotting paper wet with ammonia or acid be laid on the mandibles, the chewing movements are reversed and the object is sometimes picked up by the claws and removed. Patten found organs which he believed to be gustatory on both the mandibles and the claws (767). Pearl observed no taste reactions in the free-swimming embryo of *Limulus* (774).

§ 23. *The Chemical Sense in Insects*

Throughout all the branches of the animal kingdom thus far mentioned, the chemical sense has functioned chiefly as a food sense. There has been but little evidence of the development of qualitative discrimination within the sense itself. That is, while in many cases an animal can apparently distinguish the edible from the inedible, and gives negative reactions to irritating chemicals, one would hardly be justified in saying that it possesses more than one food sensation quality; while in our own case, of course, though we make comparatively little use of the sense of smell, the qualitative discriminations possible by its means are many. But we come now to a group of animals where there appears a remarkable development of qualitative variety in the sensations resulting from chemical stimulation; namely, the Insecta. As the reactions of animals to mechanical stimulation, on the other hand, offer evidence of little qualitative difference in

the accompanying sensations, we shall give but slight attention to them in what follows.

To begin with, there is evidence that taste and smell are distinct in many insects. The water beetle *Dytiscus marginalis*, found apparently unresponsive to food at a distance, will bite with especial eagerness at filter paper soaked in what Nagel calls "a pleasant solution" (722). Ants fed honey mixed with strychnin will taste it and then stop, and will do this even when the antennæ and mouth palpi are removed, indicating that the taste organs are in the mouth itself (308). Similar results have been obtained from similar tests on wasps, and it has been observed that wasps so treated will hesitate when offered pure honey afterward (1072).

Essenberg (284) found that the water strider, when offered flies which had been soaked, some in quinin and alcohol, some in coal oil, some in ammonia, approached them "carefully," left them, and then returned and devoured them, a proceeding which proved fatal in certain instances. The insects would stop and retreat just before reaching a drop of coal oil.

Vitus Graber tested the reactions of various insects to odors by the method which we called on page 50 the Method of Preference. This was Graber's favorite mode of studying the effect of stimuli upon animals. Applied to olfactory stimuli it consisted in offering a choice between different compartments, containing each a different odor. The animal's power of discrimination was argued from the tendency to choose certain odors rather than others. Such preferences were shown by the insects (363). The method, however, as was noted above, is unsatisfactory, because discrimination might exist where preference did not. Another criticism urged against Graber's experiments is that the odors used were too strong and irritating. There is always the possibility that such substances affect other nerves than those of smell. The insects observed by Graber displayed choice between odors even when their antennæ were removed.

There is much evidence to show that the antennæ are the

true organs of smell in insects. Various flies and beetles which are in the habit of laying their eggs in putrefying flesh will not react to it when their antennæ are removed, and it has been shown that insects which seem to find their mates by response to olfactory stimulation fail to do so when deprived of antennæ (308). Interesting "compensatory movements" have been seen in silkworm moths with one antenna removed; they turned, that is, in the direction of the remaining antenna (535). We shall note movements of this class later in insects with one eye blackened, and in fish with one auditory nerve cut. The exploring movements of the antennæ which certain insects make in seeking a proper place to lay their eggs have been taken as evidence of the smell function of these organs (786). McIndoo (628, 629, 630, 631), however, has presented evidence against the olfactory function of the antennæ. His experiments were performed on beetles, ants, honey bees, and hornets. His line of argument is as follows. While it is true that insects whose antennæ have been removed fail to respond normally to odors, this is because such insects are abnormal in all their behavior. There exist in various regions of the body of insects, as for instance the bases of the wings and legs, small pores containing sense cells; these McIndoo calls olfactory pores. He finds by measuring the time required for insects to respond to odors, that this reaction time is lengthened more decidedly when the olfactory pores are varnished over than when the antennæ are removed. Minnich (688), on the other hand, working with the cabbage butterfly, states that when both antennæ are removed, the response to olfactory stimuli by extending the proboscis occurs only 58% as often; and concludes that the antennæ are olfactory organs, but not the only ones. And von Frisch (328), having trained bees to come for food to a box carrying a certain odor, reports that they could not find the box when their antennæ were removed. That this failure was not due to the general effects of the operation appeared from the fact

that bees trained to find food on a certain color could do so after removal of the antennæ.

Von Frisch's experiments on the sense of smell in bees are more thorough than any other investigation of the chemical sense in insects. His method, as has just been said, was to place odorous substances in food-boxes, and then test the bees' learning by observing whether they would come to a particular odor even when there was no food in the box, if it was the odor previously associated with food. They distinguished in this way the fragrance of acacia from that of lavender. When trained to oil of orange peel, out of forty-three other ether oils they confused it only with bergamot and cedar; these smell like it to human nostrils, are like it found in citrus fruits, and have in common certain important chemical components. Certain odors which smell alike to man are very different in chemical composition; these seem to smell alike to bees also. However, many substances that we can distinguish are confused by the bees, and *vice versa*. Certain chemicals whose composition is the same but whose intramolecular structure is different smell different both to men and to bees. The sense of smell in bees does not seem to have a lower threshold than in human beings, but they do analyze smells better: they cease to visit the odor to which they have been trained if even a very small amount of another odor is mixed with it. To odors of the nauseous class they could not be trained.

There is evidence that solitary wasps find by smell the animal prey, caterpillars, spiders, and the like, with which they provision their nests (397). Tests show that they can find it in the dark. A wasp in search of prey will examine the silk threads left by a caterpillar on a glass plate, and assume the stinging position; she will do likewise even if the caterpillar has left no visible trace, apparently reacting to odor.

The function of the chemical sense in the mating processes of insects is one of the most remarkable phenomena con-

nected with the sensory reactions of animals. Forel says he had a female *Saturnia* moth shut up in his city room, and that within a short time a number of males came and beat against the window (308). Riley hatched in Chicago some moths from the *Ailanthus* silkworm, which were carefully confined. No other specimens were known to exist within hundreds of miles. A virgin female was put in a wicker cage on an *ailanthus* tree, and a male, with a silk thread tied around the abdomen for identification, was liberated a mile and a half away. The next morning the two were together (869).

The most interesting observations on the sense of smell as used in the mating of insects, however, are those of Fabre. A cocoon of the "*Bombyx du chêne*," a species of which Fabre had not seen a specimen in the locality for twenty years, was brought to him, and from it a female hatched. Sixty males sought her within a few hours after she reached maturity. Fabre noticed in this and other cases that shutting the female in an air-tight box prevented the males from being guided to her, but that the smallest opening was enough to allow the odor to escape; that the males were not in the least confused or led astray by placing dishes of odorous substances about, and that they would seek anything on which the female had rested for a time, a fact which suggests that the stimulus is a secretion of the body, as it is known to be in silkworm moths. Fabre offers the suggestion that smell stimuli as they are operative in the animal kingdom generally may be of two classes: (1) substances which give off particles in vapor or gas, and (2) substances which give off a form of vibration. Our own olfactory sense is limited to the first class of stimuli, but some animals, notably insects, may be sensitive to both (292). Certainly the marvellous sensitiveness involved in these mating reactions suggests a kind of response to stimulation unknown in human experience.

§ 24. *How Ants Find Food*

In many ways the Hymenoptera are the most interesting of insects, particularly those members of the order which have developed community life. Their reactions to chemical stimulation have been the subject of a large mass of literature, some of the more important results of which we may now undertake to survey, considering ants, bees, and wasps successively. Sir John Lubbock was among the earliest observers to indicate the great importance of chemical stimuli in the life of ants. In the first place, he demonstrated that it is by chemical stimulation that *ants are able to follow each other to supplies of food*; or to larvæ, for an ant's behavior to an ant larva found in the course of its wandering is like its behavior to food; the larva is picked up and carried to the nest. Lubbock put some larvæ on a glass plate at a little distance from one of his artificial ant nests, and set a similar empty plate beside it; he then made a bridge of a strip of paper leading from the nest toward the plates, and connected each of them with this bridge by a separate short paper strip. He placed a marked ant at the larvæ; she picked up one and returned to the nest. She soon appeared followed by several others; when she had reached the larvæ, and before the others had arrived at the dividing of the ways, Lubbock exchanged the short strips, so that the one over which the marked ant had passed now led to the empty plate. The following ants all took this path, indicating that they were guided by some trace which her footsteps had left. Lubbock was inclined to think, however, that some kind of communication must have passed between the marked ant and her fellows in the nest to induce them to follow her, and also that this communication might on occasion convey some notion of the quantity of food or larvæ to be had. He placed three glass plates near an ant nest, connecting each of them with the nest by means of a paper strip. On one plate he put a heap of several hundred larvæ, on the second two or

three only; the third was empty. He put a marked ant on each of the plates, and captured all the ants which they led back with them. Many more ants came to the plate with the larger heap of larvæ than to the others. Lubbock explained this by supposing that the ant from that dish had in some way communicated to the nest the greater numbers at her disposal (609, pp. 172 ff.). Obviously it would be enough to suppose that the smell of food or larvæ about an ant returning laden to the nest is a stimulus to her nest mates to follow her; that this smell is stronger, the larger the stock she has found, and hence acts as a more powerful stimulus. The question arises, however, as to how an ant can distinguish between the smell of food or larvæ on an ant that has just found a store of either, and the smell of the food and larvæ in the nest, which must adhere to all her nest mates. Some peculiarity of behavior on the part of the foraging ant would seem to be needed if she is to induce her fellows to accompany her to food. Wheeler, whose knowledge of ants is unsurpassed, but who is perhaps a little too much inclined to humanize them, says (1067, page 535), "I believe that no one who has watched ants continuously and under a variety of conditions will doubt that they actually communicate with one another. This is clearly indicated by the rapidity with which they congregate on a spot where one of their number has found food, or retire from any spot in which a few of their number have been killed or injured." Erdmann (279) says that an ant which has found booty too heavy for her to carry communicates an "alarm" to other ants by crossing antennæ with them; this incites the other ants to follow her. If the ant is imprisoned on leaving the nest after "spreading the news" in this way, the other ants cannot find the food; hence her communication furnishes nothing but a general stimulus to follow. It is interesting to note that if the booty is broken up into many small pieces such as the finder ant can carry herself, she makes no communication to the other ants, but returns again and again until she has

carried home the whole store herself. This behavior one must confess looks like that of a reflex machine; but we know that ants can learn. What concerns us just now is the fact that smell seems to play no part in these ant communications, if Erdmann is right.

§ 25. *The Use of Smell in Path-finding by Ants*

The homing of ants is a puzzling problem. Bethe (61) thinks that ants, as reflex machines, are drawn along the path back to the nest by the chemical stimulus deposited on the path by their own bodies. Piéron (794) has maintained that in some species we have to do with a kind of muscular memory, the ants simply reversing, on the homeward path, all the turnings they took on the way out, like a top unwinding itself. Cornetz (195, 196, 197) claims for ants the mysterious power of registering in their bodies the general direction of their outward course and reversing it when they have found a load to be carried home. We may consider very briefly the facts that have been brought to the support of these various hypotheses. There are really two problems involved in the homing of ants. There is, first, the problem of the homing of a solitary forager, who, having found food at the end often of a very long and rambling course, is able to get back to the nest. Secondly, there is the problem of the nature of a frequented ant road, along which many ants constantly travel to and from the nest. The evidence that smell functions in the homing process is strongest in the case of such a frequented trail. Lubbock's experiments showed that on these trails the recognition of visual landmarks plays no important part. For instance, he placed larvæ in a dish on a table connected by a bridge with an ant nest. He accustomed the ants to go back and forth between the dish and the nest by a path which he diversified with artificial scenery, such as rows of bricks along either side, and a paper tunnel. When the path was thoroughly

learned, he moved the bricks and the tunnel so that they led in a different direction: the ants, however, were not at all disconcerted by this cataclysm of nature, but followed the same tracks as before, evidently guided by their own footprints (609, p. 259). Forel (310) showed that when a piece of wood is laid across a well-frequented path of certain species of ants, they are much disturbed and at a loss to follow the trail, and Bethe (61) reports that drawing a finger across the trail will apparently break its effectiveness as a guide. That the chemical deposited by the ants is volatile he concludes from the following observation. If a strip of paper be placed across an ant path, the ants on coming to it stop, quest about, and are delayed until one accidentally runs across the strip and others follow. The piece of paper is thus gradually adopted into the ant road; if it is subsequently removed, the ants stop and are bewildered at the place where it was, showing that the earlier traces of their footsteps, under the paper, have evaporated. Again, Bethe thinks he has evidence that the chemical stimulus left by the feet of ants going from the nest is different from that deposited by those going to the nest, and that ants on the way home will not follow a track made by the feet of other ants on the outward journey, and *vice versa* (61). Bethe found that when the usual road to an ant nest had been interrupted by the removal of a heap of sand, and the road across the breach had been established solely by incoming ants, the outgoing ants refused to follow it, and made a new road for themselves (61). Wasmann thinks this may have been done merely on account of the faintness of the recently established path as compared with the old one (1041). Bethe observed also that if a strip of paper had been adopted into an ant road, and was then, while an ant was on it, rotated through 180 degrees, the ant stopped and was disturbed on coming to the end of it (61). Experiments on rotating ants were made also by Lubbock (609), and seem to give puzzling and conflicting results; it is not clear why,

even on the assumption that there is a difference in odor between the road to the nest and that from the nest, an ant on a road which led both ways should have found her course interrupted by rotation. One fact, Bethe thinks, shows that even assuming two road smells is not enough. Ants of certain families (*Lasius*) which habitually make regular and frequented roads can, if they come upon one of these roads in wandering, at once take the proper direction, either to or from the nest. Evidently the mere presence of two smells would not enable them to do this. Bethe suggests that the particles of the two chemical substances are also differently polarized, so that one of them can be followed only in one direction, the other in the opposite direction (61). Wasmann objects to this that an ant returning on its own traces would destroy them, as the opposite polarizations would cancel; and that similar confusion would occur on a narrow and much frequented road (1041). He and Forel (310) both think that, granting the discrimination between the outward and inward paths, which is made by only a few families of ants, the direction is most probably given by a perception obtained through the antennæ, of the "smell form" of the footsteps. Since the antennæ are movable organs, like the hands, they may well, Forel suggests, mediate spatial perceptions of the form and size of odorous patches. This hypothesis would fall to the ground if McIndoo's contention that the antennæ are not smell organs were sustained. Brun (123) approves of this "topochemical theory," and suggests also that the "Bethe phenomenon," as he calls the confusion of rotated ants, may be due to their experiencing a sudden change in the proportions of nest-smell and food-smell which they find on the path. The nest-smell traces would ordinarily get weaker with increasing distance from the nest, and the food-smell traces weaker with increasing distance from the food: if the middle part of the path is rotated with an ant on it, the ant on coming to the end of the rotated section would note a difference in the composition of the mixture.

On the whole, there is much evidence indicating that smell plays an important part in determining the response of ants to well-frequented roads. We may now consider the case of the solitary forager. Santschi (892) believes that he has seen a smell trail "intentionally" deposited by an ant, dragging her abdomen along the path. Bethe, whose general position that ants, and indeed all invertebrate animals, are reflex machines requires him to avoid any hypothesis that would involve learning or memory on the part of these animals, is of course anxious to explain the homing of the solitary foraging ant as a smell reflex. He placed near the entrance of a nest a large sheet of paper covered with lampblack, on which the footsteps of the ants could be traced. On this paper he put a supply of food. When an ant had found the food, Bethe reports that in returning to the nest she always followed the path by which she had come, except that when the original path had crossed itself in loops, the ant omitted the loops in her homeward way (61). Apparently, however, many species of ants do not thus retrace their own footsteps. The "muscular memory" theory of Piéron (794) is based on the observation that if a homing ant be carefully lifted and deposited at a little distance away, she will continue her course until she has traversed a distance equal to that which she would have had to go to reach her nest, if her course had not been interrupted. Cornetz's theory (195, 196, 197), that an ant has some mysterious power of retaining an impression of the direction in which she set out, and of reversing this direction when she is ready to return home, is derived from a long series of very careful field studies. He reports that a foraging ant takes a certain general direction and makes excursions to right and left in search of food. When the food has been discovered, she reverses her original direction, but does not actually retrace any part of her outgoing path. Piéron (807) is impressed by these observations, and inclined to think that a mysterious factor is actually involved. That the direction of the light may serve as a

guide in the homing of ants is indicated by observations of Lubbock (609), Turner (986), Santschi (892) and Brun (123), but the ability of ants to find their way about in the dark is sufficient proof that it cannot be the sole factor.

§ 26. *How Ants "Recognize" Nest Mates*

Another problem of ant life to which smell appears to furnish the key is that of the *recognition of nest mates*. It has long been known that an ant entering a strange nest, though of the same species, is likely to meet with rough treatment, and even be put to death. Now Forel found in 1886 that ants of the genus *Myrmica* whose antennæ were removed would attack their own nest mates (308). It seems probable that each nest of ants has a peculiar odor which is the basis of the distinction between friends and foes. Bethe tested the smell theory by dipping an ant first in weak alcohol, then in water, and then in the juices obtained by crushing the bodies of a number of ants of another species. He found that an ant thus treated would be attacked and killed by its own nest mates, but could be introduced, though not so easily, into the nest whose odor it now presumably bore, even though its appearance was quite different from that of the ants therein (61). Wasmann repeated these experiments with much less success than Bethe; bathing *Myrmica* ants with essence of *Tetramorium* ant did not preserve them from final destruction at the jaws of the latter, though it delayed their fate; nor did much bathing with foreign nest odors induce the ants to attack beetles of the species *Lomechusa strumosa*, their accustomed "guests" in the nest, though they seemed disturbed at first. Wasmann apparently thinks other factors besides smell, vision perhaps, enter into the recognition process (1041). Bethe, in a later paper, suggests that Wasmann's negative results may have been due to the fact that the nest smell very quickly returns to the ants after it has been removed; he himself took account only of the

first reaction of other ants toward the one subjected to treatment (62). Piéron (797) has repeated Bethe's experiments and confirmed his results with eighteen different combinations of ant species. Many factors, however, modify the hostile reaction to foreigners. Piéron finds that certain species are inclined to be tolerant. Attacks are more frequent near the nest than at a distance from it. A solitary ant tends to run away rather than to attack. Males do not distinguish strangers from nest mates, and a female after the marriage flight will be received in a strange nest. Brun (122) has observed that ants carrying larvæ will be tolerantly received, and that if ants from two nests are tumbled into a sack together and then tumbled out into a strange place, their hostility to each other is inhibited by their general disturbance and fright.

Termites, which, although they belong to the order of neuropterous insects and not to the Hymenoptera, have developed an organized community life much like that of ants, show the same tendency as ants to attack strangers. The young are not attacked, nor does the fighting response occur when large numbers are hastily tumbled together. That the hostile response is made to a chemical stimulus, at least in part, appears from the fact that "a well-washed termite is attacked by both aliens and fellows," but the observations do not give quite so definite results as those on ants (10).

Fielde, as the result of a study of the genus *Stenammas*, concludes that each ant is the bearer of three distinct odors: the individual odor, which enables her to follow her own trail in a labyrinth, and the reception of which depends upon the tenth segment of the antennæ; the race odor, dependent on the eleventh segment; and the nest odor, dependent on the twelfth (295). No other investigator, however, finds evidence of any such specialization of the antennal segments, and McIndoo, as we have seen, wholly rejects the antennæ as a smell organ. In a later article Fielde concludes that the nest odor of the worker ants is derived from their queen

mother; that the odor of the queen is unchanging, and is imparted to her eggs. The worker, however, gradually changes its odor. Queens of diverse odors may be produced by the influence of males that are the offspring of worker mothers and have the differentiated worker odor. A young ant isolated from the pupa stage until many days old will single out its queen mother from queens of other species, but will show decided suspicion of older sister worker ants. A mixed nest formed of newly hatched ants of different species was separated for seven months. On rejoining each other, the ants showed hostility; their odor, Fielde argues, had changed. But young ants of one species were received by those of the other species. Fielde does not hesitate to introduce the psychic factor and say that the latter remembered the odor of the young ones, having been associated with it in their own youth. The suggestion might be made that the young ants had not as yet developed any specific odor, but this is opposed by the observation that newly hatched *Lasius* ants from a strange colony were not received by a nest of *Stenammus*, while young *Lasius* ants from a colony with which the *Stenammus* had been acquainted in youth were accepted eleven months after the latter had been segregated. It is an affair of the memory, Fielde is assured; and she says, "If an ant's experience be narrow, it will quarrel with many, while acquaintance with a great number of ant odors will cause it to live peaceably with ants of diverse lineage, provided the odors characterizing such lineage and age environ it at its hatching" (300). Bethe held that an ant's own nest odor offered no stimulus to it at all, but that fighting reflexes were occasioned by any foreign nest odor (61). Many facts, however, seem to tell against this view; among others, the early observation of Forel that a *Myrmica* ant deprived of its antennæ attacks everything in sight (308). It should, according to Bethe's theory, live peaceably with all. Van der Heyde (1006) offered *Formica rufa* ants the choice between two passages leading in opposite directions; from the end of

one the odor of nestmates, kept in a box, was diffused; 81.2% of the ants chose this pathway. In other experiments the odor of ants from a foreign nest was substituted; 91.7% of the ants were attracted to this. When the two odors were used, one at the end of each path, 71.1% of the ants sought their enemies. The experimenter thinks this was due to the warlike mood produced in the ants by being handled. The experiment indicates that an ant's own nest-smell does stimulate it. Further, it is of interest in showing that smell can function as a distance sense in ants, which has been denied by some authorities, who hold that these insects must always follow smell tracks deposited on objects (283, 123).

Thus we see that in spite of some divergence of testimony, there is evidence that ants have a variety of qualitatively different smell experiences: the smell of food and of larvæ, probably distinct, though there is no experimental proof of the fact; the individual smell of an ant's own footsteps; a possible distinction, in some species, between the smell of the outgoing and that of the incoming paths; and the different odors which seem to be responsible for the discrimination between nest mates and foreigners. If it were true, as Fielde maintains, that loss of the eighth and ninth segments of the antennæ renders an ant incapable of caring for the young, then the recognition of larvæ and pupæ would depend upon a specific odor (295).

§ 27. *How Bees are Attracted to Flowers*

In bees the sense of smell is equally well developed. But no topic in comparative psychology has been more hotly disputed than the use which bees make of this sense, and the extent to which they depend, rather, upon sight. Darwin (228) and H. Müller (712, 713) thought both color and fragrance influential in attracting insects to flowers. Plateau maintains that the chief influence guiding bees to flowers is smell, and that color has little effect. He made a number

of experiments in which the brightly colored corollas of flowers were cut off without disturbing the nectaries, and claims to have found that the visits of bees to the mutilated flowers were as frequent as before (816-821). On the other hand, Giltay obtained opposite results; the flowers whose corollas were removed were neglected by bees, while those which were covered so as to be invisible but not so as to prevent the odor from escaping, were also unnoticed (352). Josephine Wéry found that the proportion of bees visiting flowers with intact corollas to those visiting flowers with the corollas removed was 66:18 (1060). Kienitz-Gerloff criticises Plateau's figures and the accuracy of his experiments (539). Forel found that a bee with the antennæ and all the mouth parts removed, hence probably incapable of smell, returned to flowers for honey, though of course without success (308). Andreaë thinks that among diurnal insects those which live on the ground, and take but short flights, are more influenced by smell; while the freely flying insects are attracted by the sight of flowers (10). On the whole, inconspicuous flowers are more often fertilized by wind than by the visits of insects. Von Frisch (328), as a result of his experiments in training bees to come to odorous boxes, concludes that smell operates only at a short distance, and that while it enables bees to identify flowers, it cannot attract them from afar. He finds another use for it in connection with honey-gathering. A bee that has found a plentiful supply of nectar, on returning to the hive, executes a kind of "round dance," which excites the other bees in her neighborhood, who sally forth in search of the food. How do they find it? They do not accompany the bee that has discovered the stock, but seek in all directions. But they note and remember the flower-smell on the discoverer. In the case of odorless flowers, the bee who finds the supply deposits on their surroundings odor from a little scent-pocket on the hinder part of her body, and this enables other bees to identify the flowers.

§ 28. *How Bees Find the Hive*

Most complicated of all is the problem as to how bees find their way back to the hive. It is obvious that the simple ant method of following a chemical trail is ruled out for insects that fly. Bethe abandons the puzzle as insoluble (61). Von Buttel-Reepen attempts at length, and with a vast amount of apic lore, to refute his position. It would be impossible to give more than the briefest statement of the arguments of both sides. Bethe maintains that the smell of the hive does not guide the bees back to it, because he found that if the hive were rotated slowly enough to allow the cloud of nest smell at the opening to move with the opening, the bees returning would not follow it for more than 45°, but would go to the place where the opening had been. He thinks they are not guided by sight, because when he completely changed the appearance of the hive, masking it with branches and other coverings, the bees were not disconcerted, but flew straight to the mouth of the hive. He brings other evidence against the vision hypothesis which we shall discuss in Chapter XI. An unknown force, he concludes, guides the bee in its homing flight (61). Von Buttel-Reepen believes that visual memory will explain all the facts; that the bees were not disturbed by the altered appearance of their hive because they knew their way so thoroughly that nothing could disturb them by the time they had come so nearly home. The visual memory required is, he admits, of a peculiar sort, which we shall consider in a later chapter. The odor of the hive does cooperate with vision in certain cases; when a stock of bees has been moved without their knowledge, they fly out without making any "orienting flight," as they commonly do on leaving a new place, a fact that is one of the evidences for the visual memory theory. Nevertheless, many of them succeed in finding their way back, and then, if their hive is placed among a number of others, von Buttel-Reepen thinks they

"smell" their way back to the right one. He mocks at Bethe's unknown force, on the ground that it must sometimes lead the bee to the hive and sometimes back to the place where food has been found (139). Bethe attempts to answer this by saying that the force acts in coöperation with the physiological condition of the animal; the laden bee follows it to the hive, the bee with the empty crop is led back to the food supply (62). Of course one may say what one pleases about the *modus operandi* of an unknown force without fear of disproof, but also without carrying much conviction.

That a mysterious sense of direction exists in the bee is concluded by Bonnier (113) from the following evidence. He first showed that bees whose eyes had been covered by pigmented collodion could go directly to their hives if they were not more than three kilometers away. Smell, however, or muscular memory, might account for this. He then attempted to demonstrate that smell was not an essential factor in guiding bees. He placed two stands carrying honey, one 200 meters, the other six meters from the hive, and marked the bees that visited each stand, proving that a given bee almost never went to both, but continued to visit the stand where it had first found honey. Here, however, sight might have been the determining influence. Wagner (1025) thinks that bees in the neighborhood of the hive are influenced by visual landmarks, but that in their longer flights they depend on a sense of direction, which seems however to be a form of visual memory. On the whole, smell would appear to be only one factor, and not a very important one, in guiding the flights of bees.

§ 29. *How Bees "Recognize" Nest Mates*

The nest smell, which characterizes each hive and prevents the reception of strangers, who are treated precisely as by ants in similar circumstances, is composed according to von Buttel-Reepen of the following odors: the individual

odor of different workers; the family odor, common to all the offspring of the same queen; the larval smell and food smell; the drone smell, the wax smell, and the honey smell. There are various ways in which the mode of reaction to a foreign nest smell is modified. If two bee stocks are placed side by side, and one has the queen and entire brood removed, it will go over to the other stock and be kindly received. One can understand that the attraction of the queen and brood odor may overcome the tendency of the foreign nest smell to repel the invaders, but it is harder to see why the more fortunate stock should allow itself to be invaded. Further, a bee laden with honey can get itself received by a foreign stock that has exchanged hives with it, where an unladen bee is attacked; here the smell of the honey may overcome the foreign smell. As is well known, two alien stocks may be united by sprinkling them with some odorous substance. The queen odor is the strongest factor in the nest smell; in swarming it overcomes the tendency to return to the old nest, and queenless swarms will join themselves to foreign swarms having a queen. The apparent attention paid to the queen while laying eggs, the gathering of workers around her trilling their antennæ toward her, suggest strongly that her odor is pleasant to them. The queen, herself, however, is perfectly indifferent to any foreign nest smell, and will beg food of any bee, even those which are angrily crowded around her cage in a foreign hive. Drones also will go from stock to stock, and are always peacefully received until drone-killing time begins. It has usually been supposed that the unrest displayed by a bee stock when deprived of its queen is due to the absence of the queen odor, and it seems almost certain that this must be a powerful influence, though von Buttel-Reepen thinks it is not the only influence, for he has observed that if the queen be replaced in the honey space, removed from the rest of the hive, the bees will quiet instantly, before the smell has had time to diffuse itself. Also, bees sometimes behave as if they had lost their queen when she

is only put in a cage, and her odor is perfectly accessible (139).

It is clear that bees as well as ants are capable of distinguishing a considerable number of smell qualities. Probably the same thing is true of the social wasps. In the solitary wasps, however, we find less evidence of a highly developed sense of smell, or rather of a great variety of smell reactions, and the solitary bees are very likely less influenced by smell than the social bees. In the interesting study of the solitary wasps by Mr. and Mrs. Peckham, it appears that sight plays a far more important rôle than smell for these insects, and the return to the nest in particular seems to be almost entirely an affair of sight (784, 785). In general, the greatest development of qualitative variety in the sense of smell is found in the social Hymenoptera, and is probably a product of the social state. Perris, however, noted that the solitary wasp *Dinetus* was much disturbed in finding its nest hole if he had placed his hand over the hole during the wasp's absence, and thought the odor of his hand was distracting to the insect (786).

§ 30. *The Chemical Sense in Vertebrates*

Although the vertebrates stand at the head of the animal kingdom, yet in point of complexity of structure and behavior the lowest vertebrate is far below the highest members of the invertebrate division. When we undertake to study the responses to special stimulation displayed by this same lowest vertebrate, the little *Amphioxus* or lancelet, it is like going back to the earthworm. The only kind of evidence that contact, chemical, and temperature stimuli produce specific sensation qualities is found in the fact that sensibility to them is differently localized, and may be independently fatigued. To weak acid, the head end of the animal is most sensitive, the posterior end less, the middle least; to contact with a camel's-hair brush, the two ends are equally sensitive

and more so than the middle; to a current of warm water the order of sensitiveness is: head end, middle, posterior end (747).

For *fishes*, as for all aquatic animals, the distinction between smell and taste becomes obscure. The neighborhood of food not in actual contact with the body seems to stir fish to activity, but not to direct their movements. Bateson (34) and Herrick (408) both obtained evidence of this; Nagel, on the other hand, declares that fish do not perceive food at a distance except by sight, and that the function of the first pair of cranial nerves in these animals must remain uncertain (722). The well-developed character of these "olfactory" nerves and lobes, whose function in higher vertebrates is certainly connected with smell, would argue against the supposition that smell can be wholly lacking in fishes. It is generally agreed that a contact food sense exists in fish; Nagel, however, holds that its organs are situated only about the mouth (722), while Herrick has good experimental proof that fishes which have "terminal buds," structures resembling taste buds, distributed over the skin, are also sensitive to food stimulation applied to different regions of the skin. He thinks that Nagel's negative results were due to the fact that instead of food stimuli in his experiments he used chemicals with which the fish would not normally be acquainted (408).

Parker (752), experimenting with catfish and the young of a species of lamprey, found the whole body surface more or less sensitive to salt, acid, and alkali; the body of the lampreys was sensitive also to quinin solution, but that of the catfish was not; neither animal displayed skin sensitiveness to sugar solution. Cutting the nerve supply to the olfactory organs, the lateral-line organs (see page 117), and the taste buds failed to abolish skin sensitiveness, which Parker therefore concludes must depend on free nerve endings in the skin. He distinguishes three forms of chemical sensibility in these lower vertebrates: common chemical sensibility, for which free

nerve endings are the organ; taste, dependent on the taste buds; and smell, dependent on the olfactory nerves, and responding to much more dilute solutions than the other two, thus being capable of acting as a distance sense (756). Strieck (946) has ingeniously shown the capacity of the small fish *Phoxinus* to discriminate sweet, salt, bitter, and sour. The fish was given pieces of meat sweetened, along with pieces of cotton soaked in meat juice and in either salt, sour, or bitter solutions. In three or four weeks they learned not to seize the cotton: they were then offered cotton soaked in sugar solution and promptly took it. Similar training succeeded when the meat had been treated with bitter, salt, or sour substances. Extirpating the olfactory lobes did not affect the response, which is concluded to be a true taste discrimination.

Olmsted (733) has tried to determine the exact chemical character of the smell stimulus for catfish. They bite at bags containing bits of earthworm, beef-liver, or clotted blood; these responses cease when the olfactory apparatus is eliminated, but are unaffected by blinding or loss of the barbels. The essential stimulus seems to be protein, for the fats and volatile oils of the substances were non-stimulating, and so was decayed animal matter, in which the proteins are destroyed; but the stimulating proteins must be present in very small quantities, for they could not be detected by ordinary tests. A number of species of fish have been shown to possess smell, by demonstrating that they can discriminate between small bags filled with food and similar bags stuffed with inedible substances, and that this discrimination is lost when the olfactory nerves are cut or the nostrils are closed (753, 193). Shelford and his associates (920) have thrown light on a very interesting problem in animal behavior, the migrations of fish. It is well known that salmon return to fresh water to spawn, ascending rivers, and that other fish perform migrations that are of great economic importance to the fishing industry. Shelford has demonstrated that fish are very

sensitive to slight variations in the chemical constitution, the salinity, for instance, of the water in which they live, and their responses to such changes may well account for all their wanderings.

Among *amphibians*, the spotted newt seems to show a relation between smell and the "common chemical sense" not unlike that existing in fishes. The olfactory nerves seem to be required for the discrimination of food. When chemicals are applied to the body, the head end is much the most sensitive region, even when the olfactory nerves are cut. Acids and alkalies cause very marked reactions; salt is less effective and sugar not effective at all (849). Cole (181) studied the time required for the reflex withdrawal of the hind legs of leopard frogs when four chlorides, those of ammonium, potassium, sodium and lithium, were applied in solution. He found that the speed of reaction corresponded to the order in which these salts affect the human sense of taste. That a common chemical sense, and not pain, was involved in these skin reactions was indicated by the fact that they persisted when ordinary pain reactions, to pricks, were abolished by cocaine. Risser (870) reports that while sight seems to be more important than smell in determining the mature toad's reactions to food, tadpoles failed to distinguish packets containing food when their nostrils were plugged. Immature *Amblystomas*, which in the normal condition react positively both to motionless food and to moving inedible objects, lost the first type of response when their nasal pits were removed, and the second type when their eyes were operated on (136). Nicholas (725) has shown that *Amblystomas* with a collodion mask over their nostrils are delayed in finding food. The salamander *Triton* gives an odd reaction when food is placed in the water: it puts its nose on the ground and moves all around the neighborhood; if very hungry, arching the body so that only the nose and the tips of the toes on one side are in contact with the ground. This response is absent if the olfactory nerve is cut, and

occurs only when the stimulus reaches the nasal cavity (665). In its later, land-dwelling phase, Triton can find buried food by smell: the same sense-organ serves for both liquid and gaseous stimuli (666). This salamander can find resting food only by smell; none but moving objects arouse response through sight (667). The method used by Strieck to demonstrate discrimination by fish of sweet, salt, sour, and bitter tastes, has given the same result in the case of certain salamanders (351).

In *birds* sight and hearing are so well developed that the chemical sense assumes less importance. Birds seem to have a sense of taste: the chicks experimented on by Lloyd Morgan, for example, showed disgust on picking up bits of orange peel instead of yolk of egg (703, pp. 40-41). Herring gulls make similar manifestations on being fed salt fish, and take bread soaked in meat juice more readily than water-soaked bread (947). Raspail (846) thinks that birds abandon eggs which have been handled because they detect the fact by smell; that they find buried grubs by smell, and are guided by this sense to concealed food and water. The last statement he supports by the observation that their tracks lead straight to hidden food on their first visit to it, showing that it was not found by accident. Strong (946) made a careful study of the olfactory apparatus in twenty-seven of the thirty-five existing orders of birds. He concludes that "the olfactory organs of birds are of too great size to be set aside as non-functional," but that as one passes from the lower to the higher orders of birds there is a tendency towards retrogression in these organs. The crow family, sometimes considered to be the highest birds, show extremely minute smell organs. "The sense of smell has evidently been disappearing in birds with the great development of vision." The hypothesis has been put forward by Cyon (223) that smell may somehow function in guiding the long flights of birds. Watson (1050) found that the noddy tern could find its way from Key West to its nest on the Tortugas with the nostrils tightly sealed.

Strong, however, points out that this bird has very small olfactory organs, and thinks it possible that other birds may make more use of the olfactory sense in homing and migrations. The fulmar, for instance, is a bird which makes very long ocean flights, and has an enormously developed olfactory apparatus. Strong (946) made experiments with the ring dove in which he was apparently able to establish some association between the smell of bergamot in a certain compartment and the choice of that compartment as containing food.

When we come to the *Mammalia*, we find in the great majority of types a very high development of qualitative discrimination in the sense of smell. Hunters know it to be the chief defensive weapon of wild animals, and it has retained great keenness in many domesticated ones,—the cat, for instance, which will be awakened from slumber in the garret by the odor, quite unsuspected of human nostrils, of some favorite food being prepared in the kitchen, and is thrown into ecstasy at a faint whiff of catnip. The dog, however, is the hero of this field of mental prowess. The experiments of Romanes on the power of a favorite setter to track his scent are well known. In one of them he collected a number of men, and told them to walk in Indian file, "each man taking care to place his feet in the footprints of his predecessor. In this procession, numbering twelve in all," Romanes says, "I took the lead, while the gamekeeper brought up the rear. When we had walked two hundred yards, I turned to the right, followed by five of the men; and at the point where I had turned to the right, the seventh man turned to the left, followed by all the remainder. The two parties . . . having walked in opposite directions for a considerable distance, concealed themselves, and the bitch was put upon the common track of the whole party before the point of divergence. Following this common track with rapidity, she at first overshot the point of divergence, but quickly recovering it, without any

hesitation chose the track which turned to the right." It had previously been ascertained that she would not follow the scent of any other man in the party save her master, and failing him, the gamekeeper. "Yet . . . my footprints," continued Romanes, "in the common track were overlaid by eleven others, and in the track to the right by five others. Moreover, as it was the gamekeeper who brought up the rear, and as in the absence of my trail she would always follow his, the fact of his scent being, so to speak, uppermost in the series, was shown in no way to disconcert the animal following another familiar scent lowermost in the series" (875). These observations have been confirmed by the experiments of Buytendijk (146). The World War increased interest in the breeding and training of dogs to track human beings by scent. Loehner (607) has recently studied the abilities of German police dogs; he used pieces of wood, all alike, and handled by means of forceps. One piece was held in a given person's hand, and then put among the others while the dog was not looking. The dog was then allowed to smell the hand, and required to find and bring the piece of wood that had been held. The process of deodorizing the sticks between experiments was carefully worked out. The dog could succeed even if the stick was held only for one or two seconds, and if it was merely touched with a finger-tip. He succeeded when other persons handled the stick after the one whose scent was to be identified, and when artificial odors were daubed on the stick, although he barked his disapproval. He could identify the odor of an individual although the stick had been placed on different parts of the body. Buytendijk (146) reports that the police dog he tested did best when the objects it had to investigate were all of the same kind. He finds that the dog can discriminate between mixtures of artificial smells which are indistinguishable to man. Such behavior indicates not only that the dog can experience a variety of smell qualities, which is also the case with us human beings, but that it has the power to analyze a smell fusion and attend exclusively to

one component, a power that we lack almost entirely. When we experience two smell stimuli at the same time, it is but rarely that we can detect both of the qualities in the mixture; usually one of them swamps the other, or else a new odor unlike both results. But the dog, and probably many other animals, can analyze a smell fusion as a trained musician analyzes a chord. In this respect, if not in the variety of smell qualities, the olfactory sense has undergone degeneration in us: creatures that have removed their noses so far from the ground cannot hope to use smell as a topochemical sense, and hence must be at a disadvantage in analyzing compound smells. Certain authorities (*e.g.*, 913) have maintained that dogs can distinguish only animal smells, because only such odors make them sniff. Henning (401), however, using the Multiple Choice Method (see Chap. XI), reports that the dog could perfectly discriminate among a variety of perfumes and plant fragrances. He argues that the dog sniffs only when he gets an odor of vital importance to him, but can perfectly well detect other odors.

Monkeys seem to resemble us in their dependence on sight rather than smell in finding food. Kinnaman (540) reports that the monkeys he tested with regard to their power of discriminating the size, shape, and color of vessels in one of which food was placed, always looked, never smelled, for the food. And Koehler says of apes: "Anthropoids have this sense to a very limited degree; a hidden pear, tomato, or the like . . . is not smelt a couple of decimetres away" (553, p. 292).



Here

CHAPTER VI

SENSORY DISCRIMINATION: HEARING

§ 31. *Hearing in lower invertebrates*

THE sense of hearing, in all air-dwelling animals, is that sense whose adequate stimulus consists in air vibrations; for human beings these vibrations may reach a frequency of 50,000 (single vibrations) in one second and still produce an auditory sensation. But the meaning of the term "hearing" for water-dwelling animals, and hence for most of the lowest forms of animal life, is more difficult to determine. In the Protozoa it seems to have no meaning at all; the reactions of these animals to water vibrations are indistinguishable from their reactions to mechanical stimulation. But in some of the cœlenterates the possibility of a specific auditory sensation quality has been suggested by the discovery of a peculiar *sense organ*. While varying in its structure in different genera and orders of cœlenterate animals, this organ consists typically of a small sac, filled with fluid and containing one or more mineral bodies. Apparently these latter could operate in connection with a stimulus only when the stimulus was constituted by shaking the animal, or in some way disturbing its equilibrium. They might then serve as means for the reception of water vibrations, as the ear serves for the reception of air vibrations; they might, in short, be primitive organs of hearing. Accordingly the term "otocysts" was given to organs of this type wherever they were found in the animal kingdom, and the mineral bodies in the otocysts were called otoliths.

But experiments upon cœlenterates have entirely failed to show that animals of this class react to sounds (277, 1010, 721). And in some cœlenterates, as well as in higher animals

having the same type of organ, the removal of the so-called otocysts has been found to involve disturbance of the animal's power to keep its balance and maintain a normal position. Hence Verworn has suggested that for "otocyst" and "otolith" the terms "statocyst" and "statolith" might appropriately be substituted (1010). In jellyfish, indeed, even the balancing function of the statocyst organs appears doubtful; and it is possible that they function in response to shaking and jarring (714, 721). In any case, there is no evidence whatever of a specific auditory sensation in the consciousness, if such exists, of coelenterate animals.

Nor has any reaction to sound been demonstrated in either the flatworms or the annelid worms; their sensitiveness to vibrations seems to be an affair of mechanical stimulation. Darwin's experiments on this point are well known. The earthworms which he observed were quite insensitive to musical tones, but when the flower pots containing their burrows were placed on a piano, the worms retreated hastily as soon as a note was struck (229). Most observers agree that mollusks also react only to mechanical jars (*e.g.*, 259), and that the statocyst organs found in some mollusks have no auditory function. Bateson, however, records that a certain lamellibranch, suspended by a thread in a tank, responded by shutting its shell when a sound was produced by rubbing a finger along the glass side of the tank (34). The echinoderms are apparently insensitive to auditory stimuli (835, 873).

§ 32. *Hearing in Crustacea*

In the Crustacea the function of the statocyst organs has been the subject of much dispute. They are in this group of animals sometimes closed sacs with statoliths, sometimes open sacs containing grains of sand. Most commonly the organs are situated in the basal segment of the small antennæ. There is usually inside the sac a projection bearing several ridges of hairs, graded in size, which tempt to the hypothesis that

they respond to vibrations of different wave lengths, as the fibres of the basilar membrane of the human cochlea are supposed by the Helmholtz theory to do. Hensen, indeed, placing under the microscope the tail of a small shrimp, *Mysis*, whose statocyst is situated in that region, observed that the long hairs of the tail vibrated in response to musical tones, from which he infers that the statocyst hairs may do so¹ (404). In 1899 he was still inclined to believe that the latter can serve no other than an auditory function (405). Nevertheless the weight of authority is in favor of regarding the "sac" in Crustacea as a static rather than an auditory organ. The only evidence of sound reaction in two shrimp-like forms, *Palæmon* and *Palæmonetes*, was a "flight reflex" given by some individuals when sounds were produced very near them in the water; and although this response ceased when the statocysts were destroyed, the fact is of little significance, as other reflexes also were abolished by the operation (47). To sounds made by tapping the wall of the aquarium *Palæmonetes* reacted by leaping away from the wall nearest to it, even though the leap was made toward the sound. When both statocysts were removed, the reactions were still made, but not so markedly nor at so great a distance from the sound. A similar response to the striking of a partially submerged glass jar was seen in a decapod, *Virbius zostericola*, which has no statoliths (834). *Mysis* has been found to react to sounds when the statocysts are destroyed (58). The fiddler crab, which is amphibious, responds in water to vibrations by retreating slowly from the vibrating walls, and does the same when blinded and deprived of its statocysts, but gives no reaction when the antennæ and antennules are removed. On land these animals do not respond to sounds, only to vibrations produced in the earth, for instance by stamping (834). No sound reactions have been found in the crayfish (49). In short, such

¹ This observation is sometimes incorrectly quoted as if the hairs concerned were actually the statocyst hairs. Cf., for example, Morgan, 701, p. 266.

responses to vibrations as occur among the Crustacea seem affairs rather of mechanical than of true auditory stimulation; nevertheless Bethe (58) and Hensen (405) are both inclined to believe, as did Delage, who first called attention to the static function of the statocysts (244), that they may be auditory organs also. The "static sense" of Crustacea will be discussed later.

§ 33. *Hearing in Spiders*

In spiders the same difficulty arises, of deciding whether the reactions to sound are tactile or auditory. There are no statocysts, but the delicate hairs on the body and legs of the animal have been held to be auditory organs. Dahl, a number of years ago, found them responding to the tones of a violin (224, 225), but this test, which Hensen applied to Mysis, is of very doubtful significance; as Prentiss suggests, the hairs on the back of the human hand do the same (834). When various species of spiders were tested by holding tuning forks near them or their webs, only the web-making species gave any response. These latter would not react to ordinary noises, nor to the sound of a small fork, but to the humming of a large fork they responded always by raising the front legs, and sometimes by dropping from their webs (782). Two Texan species that were experimented upon by placing them in a cage free from vibration gave no response whatever to tuning forks of various pitches or to other sounds (837). It seems, then, highly probable that spiders are sensitive only to vibrations communicated to their webs, and very likely these furnish tactile rather than specific auditory stimulation. The observation of Boys may be quoted: "On sounding an A fork, and lightly touching with it any leaf or other support of the web or any portion of the web itself, I found that the spider, if at the centre of the web, rapidly slews around so as to face the direction of the fork, feeling with its fore feet along which radial thread the vibration travels. Having become satisfied on this point, it next darts along that thread till it

reaches either the fork itself or a junction of two or more threads, the right one of which it instantly determines as before. If the fork is not removed when the spider has arrived it seems to have the same charm as any fly, for the spider seizes it, embraces it, and runs about on the legs of the fork as often as it is made to sound, never seeming to learn by experience that other things may buzz besides its natural food. If the spider is not at the centre of the web at the time that the fork is applied, it cannot tell which way to go until it has been to the centre to ascertain which radial thread is vibrating." If, however, it has followed the fork to the edge of the web, and the fork is then withdrawn and brought near again, the spider reaches out in its direction. If the spider is at the centre of the web and a sounding fork is brought near without touching the web, the spider does not reach for it, but drops down at the end of a thread. If the fork touches the web again, the spider climbs the thread and finds the spot very quickly (116).

§ 34. *Hearing in Insects*

The sense of hearing in insects also is problematical. When the insect makes a sound itself, which, as in the case of crickets, is connected with the mating process, it would seem *a priori* highly probable that it can hear. Various structures have been designated as auditory organs, the finely branched antennæ of mosquitoes and gnats, on the same doubtful evidence that they have been found to vibrate in response to musical tones (670); and in the Orthoptera certain very peculiar structures situated on the front legs of grasshoppers and crickets, and in the first segment of the abdomen in locusts. These structures Graber called chordotonal organs, and he felt convinced from experimental tests that they were auditory. The cockroach, *Blatta*, while running about the room will stop, he says, for an instant when the strings of a violin are struck. A blinded specimen, hung by a thread, became vio-

lently agitated at a sudden tone from a violin. A water insect, *Corixa*, although undisturbed by the water vibrations produced by pushing a bone disk toward it in the water, gave decided reactions when the disk was connected with an electric bell. Other water beetles were still more sensitive. That they distinguished pitch differences Graber thought probable from the fact that he observed reactions of different degrees of violence to sounds of different pitch; and their discrimination of intensity changes he thought demonstrated by the fact that if a continuous tone, sounding while a water beetle is swimming about, be made suddenly louder, the speed of the insect's movements visibly increases. It is going rather far, however, to pass from the evidence that insects discriminate sounds made by their own species from other sounds to the conclusion that "they like us have the capacity to analyze, at least to a certain degree, these peculiar clangs or noises, and to distinguish clearly from one another the partial tones that compose them" (359).

Tower thought that he had observed the potato beetle reacting to the sound of a tuning fork (978). Will noted responses from a male beetle to the stridulation of a female of its species enclosed in a box 15 cm. away (1072). Rádl made the suggestion that the organs which Graber called chordotonal organs, and which contain a fibre stretched between two points of the integument, represent a kind of transition between "*Gemeingefühl*," that is, organic and kinæsthetic sensations, and hearing. In support he offers the following evidence: the fibres resemble the tendons in which some muscles end, and are very likely developed from tendons; the organs exist in insects that have no use for hearing, such as grubs shut up in fruits; insects have not been shown to respond to pure tones, but only to noises, such as the cricket's chirping, which for us affect *Gemeingefühl*. Further, there is no evidence that hearing ever guides insects to each other; in short, it is but a rudimentary sense, and its organs are those which serve also to register muscular activity. It is, in insects, a

"refined muscular sense" (844). Regen (854) demonstrated very prettily an apparently auditory reaction in the female cricket. He placed in the centre of a wide area on the floor two glass vessels, one lined with black paper, the other transparent. In the opaque vessel he placed a chirping male; in the transparent vessel a quiet male. Normal females ran to the vessel which contained the chirping male, but ignored the other vessel: females whose "tympanal organs" on the forelegs had been operated on did not react to either vessel. That the response was not to an odor liberated by the movement of the male's wings in chirping, was shown by removing the edges of the wings, so that their motion, while otherwise unchanged, was noiseless: the response of the females ceased.

It seems likely that the auditory sense, if it exists in insects, would be confined to those which produce sounds, and its qualities limited within the range of such sounds. Turner (996), however, finds that silkworm moths, alighted on hanging shelves and thus protected from jarring, respond by waving their wings when an organ pipe, a pitch pipe, and various notes on the Galton whistle are sounded. One species, which failed to respond, he rendered more excitable by rough handling, and then succeeded in stimulating the sound reactions. Several different species of *Catocala* moths were found to respond to high notes on the Galton whistle, either by flying or by quivering their wings. By touching the insect at the moment when the tone was sounded, thus giving it a "life significance" to the insect, some of the moths were trained to react to a lower organ tone (256 vibrations) even when they were not touched. These moths are not known to make sounds (998).

Noctuid moths react, when in an active condition, to various sound stimuli, either by taking flight or by lifting their wings. When the tympanal organs, between the thorax and abdomen, are injured, the reaction ceases except when the sounds are very loud. Moths with one-sided destruction of the tympanal organ reacted in seven-tenths of the tests (271).

Minnich (689) has studied reactions to sounds in the caterpillars of a butterfly, taking accurate precautions against giving them any mechanical stimulation; he found that they respond to tone stimuli by jerking up the front third of the body. The upper pitch limit was about 1024 vibrations. That the sense-organ is certain hairs on the front two-thirds of the body, he showed by demonstrating that singeing these hairs, or loading them with flour or drops of water, either greatly reduced the response or abolished it.

Most species of ants produce no sound that the human ear, even with the aid of a microphone (609), can detect, although certain East Indian species are reported to make a loud hissing noise when disturbed (1039), and some American species are said to chirp (274, 1066). Ch. Janet maintains that ants of the *Myrmicidæ* make a stridulating noise (491, 492). The weight of evidence is against the existence of sound reactions in ants; careful experiments by Fielde and Parker on a number of species led to the conclusion that the only vibrations responded to were those which were communicated through the solid on which the ants stood, and received through the legs (302). It is probable that the observers who have come to opposite conclusions have not in every case been careful to exclude the possibility of such vibration of the substratum. Wasmann, for instance, thinks he has seen reactions to sound; he noted that ants in an artificial nest raised their antennæ and lifted the fore part of their bodies when he scratched with a needle on some sealing wax with which the nest had been mended (1038). He also quotes Forel's account (307) of a species which makes an "alarm signal" by striking the ground with its abdomen: this, remarks Wasmann naïvely, must be perceived by the ants, "otherwise it would not be an alarm signal"! (1039). If perceived, it may of course be as a tactile rather than an auditory sensation. Weld has observed reactions to the sound of whistles and tuning forks in several species of ants, and even concludes that they perceive the direction from which sounds come; but since, of the four ob-

servations upon which this latter opinion is based, two were cases where the ants hurried toward the sound and the others cases where they backed away from it, the possibility of mere coincidence seems not to be excluded (1057).

As regards the auditory sense in bees, von Buttel-Reepen, who knows them well, thinks it plays a considerable part in their lives. He believes that the disturbance produced by the loss of a queen is communicated to the whole hive by the peculiar wailing noise made by some members and instinctively imitated by the others, and that this disturbance is calmed by a similar dissemination of the "happy humming" produced on her restoration—hearing playing a more important part than smell. The starting of a swarm, he thinks, is also largely a matter of sound communication. The process begins by the coming out of certain bees which push in among the bees hanging at the entrance of the hive and stir them up to swarming by making sounds. The "swarm-tone" is peculiar and often disturbs the inhabitants of neighboring hives that are not ready to swarm. Also, a swarm can be guided to a new dwelling if a few bees are taken there; they call the others by loud humming. If during this process the new hive is moved, the bees will go on for a few moments in the direction in which they started, then slowly turn, guided by the tone. A few may keep on in the original direction. We may look with suspicion, however, upon von Buttel-Reepen's suggestion that these latter, having passed beyond hearing of the call, are guided by the recollection of the tone they heard at first! He refers also to the shrill noise made by the young queens ready to swarm, and to the peculiar uneasiness produced when a strange queen is being attacked, and resulting, he thinks, from her "cries of pain" (139).

McIndoo (632) finds a special sound-producing apparatus in the bee, the membrane lying between the axillaries at the base of the front wings, that is responsible not for the ordinary buzzing, which comes from wing movements, but for the "high squeal" given by a squeezed bee. He is skeptical,

however, about hearing in bees; their only possible auditory organs, the chordotonal, lack the external tympanum present in crickets and katydids. And the weight of evidence seems to be on the negative side. Lubbock (609) failed to get bees to respond to any artificially produced sounds. Bethe (62) and Forel (308) believe them to be deaf. More recently Armbruster (12, 13) reports observations tending to show that they do not hear the sounds they make, and experiments, continued by Kröning (563), proving that they do not hear artificial sounds of the same pitch range as their own. The method was that of associating a food-box with a tone stimulus produced from a cathode tube.

Thus the evidence for hearing in insects is conflicting.

§ 35. *Hearing in Fishes*

Throughout the vertebrate animals there exist structures bearing analogy to our own ears, whose function might therefore be supposed to be auditory. But in the lowest vertebrates the only structures of the human ear represented are the semicircular canals, and these suggest a static rather than an auditory organ. The cyclostomes, eel-like and semiparasitic forms classed below the true fishes, have a pair of sacs one on either side of the head, containing mineral bodies, and each leading into one or two semicircular canals. In the true fishes the sac has two chambers, marked off from each other by a constriction. Three semicircular canals open from the foremost chamber, two lying in the vertical plane, and one in the horizontal plane. The chambers contain "statoliths" and fluid.

That the semicircular canals in fishes have a static ¹ function has been shown by experiments to be described later. Is the fish ear also an organ of hearing? Again authorities disagree,

¹The word "static" is here used to mean "relating to equilibrium" in general, not to static equilibrium as distinguished from dynamic equilibrium.

and it is probable that species differ. Kreidl got no response from goldfish when vibrating rods were placed either in the water or in the air near the water. Only when the fish were made more sensitive by strychnin did they react, and only to noise, not to tone. They reacted quite as well, moreover, when the ears were removed; whence it was concluded that their sensitiveness to noise resided in the skin (560, 561). A similar negative conclusion regarding auditory sensation has been reached by F. S. Lee (580), by O. Körner as a result of experiments on twenty-five species (554), and by Marage (639), using vowel sounds sung on notes ranging from C_2 to G_6 , transmitted through rubber tubes, the tests being made on eight species. On the other hand, Bigelow found that the goldfish on which he experimented were sensitive in their normal condition, but insensitive when the auditory nerves were cut, and thinks that Kreidl's operation did not remove the whole of the fish's ear (68). Triplett thought both perch and goldfish were excited by the sound of whistling, which usually preceded their being fed (979). Parker tested the killifish, a species of minnow, using the sustained slow vibrations (40 complete swings per second) of a bass viol string placed on one side of the aquarium as a sounding board. The fish cage was suspended in the aquarium from an independent support. Normal fish responded to the vibrations, usually by movements of the fin, 96 per cent. of the time. Fish in which the nerves to the ears had been cut responded in 18 per cent. of the tests; those in which the skin had been made insensitive, but the ears left, in 94 per cent. Since causing the string to vibrate jarred the whole aquarium somewhat, these experiments were checked by others where the stimulus was produced by placing the stem of a vibrating tuning fork against the sounding board. The results were the same as in the first set of tests. Parker concludes that the ears of the minnow are certainly organs for the reception of sound; but as he obtained no such reactions from dogfish, he is inclined to think that different species vary

(741, 742). In later experiments (750) on the dogfish, Parker finds that individuals with the "auditory" or eighth nerve cut show diminished sensitiveness to the blow of a pendulum, the force of whose impact on the walls of the aquarium could be measured, while cutting the optic nerve or cocainizing the skin has no effect on the responses to these stimuli: his conclusion is that the reactions are auditory. In the squeteague (748), he infers from the results of operation that one part of the ear, the utriculus, functions in the maintenance of equilibrium, while the other part, the sacculus, is the organ of hearing. The otoliths, or statoliths, in the ears of the squeteague and dogfish Parker thinks have actually an auditory function, contrary to what is known of their use in invertebrate animals; when they were removed from the ear of the dogfish, he reports, there was no disturbance of equilibrium, but a reduction in the reaction to blows on the aquarium wall, and when the large otolith in the sacculus of squeteague was pinned down, a similar result was obtained. Most sounds made in the air are extremely faint under water, but to sounds really propagated through water, Parker thinks many fish are sensitive. Certain sounds may actually attract them: the squeteague, for instance, itself makes sounds which may serve to bring the sexes together. Tests by Zenneck on *Leuciscus rutilus*, *L. dobula*, and *Alburnus lucidus* also led to the conviction that these fish, at least, could hear. A bell was struck by electricity under water, and occasionally a piece of leather was placed upon it at the point where the clapper struck. In the latter case, the mechanical vibrations produced were, it was held, the same as those occasioned by the actual ringing of the bell, but the sound vibrations were destroyed. The fish reacted by swimming instantly away from the neighborhood of the bell when it was rung, but not when the leather was used; hence, apparently, they reacted to sound (1134). These experiments, however, have been repeated on trout and eels by Bernoulli (53) with negative results.

McDonald (624) taught a group of minnows to come for

food at the sound of a bass viol string of 96 v., stretched across the aquarium, proper precautions being taken against the use of sight. Westerfield (1061) trained eight minnows to distinguish between a note of 288 v., associated with a bit of snail in a forceps, and a "high note" associated with a bit of gray filter paper soaked in camphor: that sound was the actual clue was shown by the fact that the fish subsequently ignored the actual food stimulus when it was presented with the high tone. Froloff (341) has taught fish to associate sounds with electric shocks.

Widely distributed among fishes is a curious set of structures known as the lateral-line canals. Along each side of the fish, extending from head to tail, there is a row of pores opening into a long canal, which at the head divides into three branches, one going upward above the eye, a second below the eye, and a third down toward the lower jaw. The functions of these canals have given rise to much discussion among zoölogists, an exhaustive history of which will be found in Parker's monograph entitled "The Function of the Lateral-line Organs in Fishes." Parker first proved experimentally that the canals played no part in responses to the following stimuli: light, heat, salinity of the water, food, oxygen dissolved in the water, carbon dioxide, foulness of the water, hydrostatic pressure, steady currents flowing through the water, and sound. When, however, the water in the aquarium was made to vibrate slowly, about six times per second, the fish made certain characteristic reactions, differing somewhat for the four or five species observed, but always failing to appear when the lateral-line nerve was cut. Parker concludes that "the stimulus for the lateral-line organs (a water vibration of low frequency) is a physical stimulus intermediate in character between that effective for the skin (deforming pressure of solids, currents, etc.) and that for the ear (vibrations of high frequency), and indicates that these organs hold an intermediate place between the two sets of sense organs named" (745). The ear is thus regarded as actually derived

from the lateral-line canal, as this in turn was derived from the skin. We may suppose that at least three different sensation qualities result from stimulation of the skin, the canals, and the ear, where hearing can be shown to exist.

Hofer (452) criticizes these experiments on the ground that when Parker cut the lateral-line nerves he also destroyed the nerves supplying the skin of the head, a particularly sensitive region to touch stimuli. It is, according to Hofer, the skin nerves that are affected by the slow vibrations which Parker thought to be the proper stimulus for the lateral-line organs, and in certain cases he demonstrated that such stimuli were responded to when the lateral-line organs had been destroyed. The true function of the lateral-line organs Hofer finds to be that of response to streaming movements in the water. A skin sensitiveness to currents would be of the greatest practical value in guiding the fish's migrations.

Manning (638) has carefully analyzed the functions of various possible sound-receiving organs in the goldfish, using tones of accurately controlled frequency, transmitted to a telephone receiver submerged in the aquarium. The following operations on the ear were performed: removal of the utricle and semicircular canals, removal of the saccule and lagena, removal of the whole ear. The fish were responsive from 43 to 2752 complete vibrations per second. Up to 344 vibrations, the skin and possibly the lateral-line organs were receptors; from 43 to 688 vibrations the utricle seemed to be involved, and the saccule with the lagena above 688 vibrations. Injections of strychnine heightened the range of skin sensibility to 688 vibrations.

On the whole, it appears that fish can hear, when the sound vibrations are actually communicated to the water.

§ 36. *Hearing in Amphibia*

The young of *Necturus*, commonly known as mud-puppies, have shown an increase in the rate of their gill-movements at

the sound of wires vibrating 120 or fewer times a second, and these responses ceased when the nerves supplying the lateral-line organs were cut (268). Emergence from the water on the part of adult Amphibia is accompanied by disappearance of the lateral-line canals, and consequently of whatever sensations these mediate. In the frog, the ear has a tympanic membrane lying at the surface of the head. A single bone, the *columella*, with one end against this membrane, lies across the middle ear. The internal ear is not essentially different in structure from that of the fish; there is no cochlea. Yerkes has made an interesting study of the reaction of frogs to sound. He found that they occasionally "straightened up and raised the head as if listening" when other frogs croaked or made a splash by jumping into the water. To no other sound did he get any apparent response, nor was it possible to make frogs in their native habitat jump or show any uneasiness by producing any sort of noise, so long as the experimenter remained invisible. "Apparently," Yerkes says, "they depend almost entirely upon vision for the avoidance of dangers." It is of course highly improbable that an organ should be adapted only to the reception of the croaking of other frogs and the splash of water, and not to noises made in imitation of these; and Yerkes suggests that the frogs may hear many sounds to which they respond by inhibiting movement as a measure of safety. This view is confirmed by the results of experiments where the breathing movements of the frog's throat were registered by means of a lever resting against it and recording on smoked paper. Evidence from change of the breathing rate was obtained of the hearing of sounds ranging from fifty to one thousand single vibrations a second (1100). Later, it was shown that sounds, although they did not, when given alone, cause the frogs to react, modified the responses to other stimuli, reinforcing or inhibiting them according to the interval between the sound and the other stimulus. This effect was noticed both when the frogs were in the air and when they were under water. It was more marked in the

spring (the mating season) than in the winter. That it concerned the special auditory sense-apparatus, and hence may have been accompanied by true auditory sensations, was shown by the fact that it disappeared when the auditory nerves were cut. Sounds ranging from fifty to ten thousand single vibrations a second were effective (1108, 1110). This, of course, does not mean that the frog perceives such sounds as differing in pitch.

§ 37. *Hearing in Higher Vertebrates*

The auditory sense in many reptiles seems to be absent or defective, so far as investigation has yet gone. Manning (637) experimented on a considerable number of rattlesnakes, belonging to several species; watching for the response either of rattling or protrusion of the tongue, and using sounds of 43, 86, 172, 344, 688, 1376, and 2752 double vibrations as stimuli. The results were practically always negative unless the vibrations were communicated through the substrate on which the snakes rested, and hence capable of affecting touch. It is very doubtful, he says, whether a rattlesnake ever heard its own rattle! Kuroda (568) has failed both in getting reactions to various sounds from the turtle *Chlemys japonica*, and in teaching it to associate either food or electric punishment with sounds. He succeeded, however, in causing a lizard to betray sensibility to sound, by the following amusing method. When the lizard (*Tachydromus*) is left undisturbed, it closes its eyes, and at intervals opens them again. The time of five successive such intervals was taken; the average was 35.6". The experimenter then blew a Galton whistle about 10" after the animal closed its eyes, whereupon it opened them; this occurred repeatedly. The upper limen was found to be 10,000 vibrations. Lizards of the class *Lacertilia* respond to sounds by opening their eyes, and by a change in the breathing rate; they can also be trained to look up at the sound of a whistle towards the place from which they are accustomed to have food dropped to them.

Their upper limit was 8000 d.v. In crocodiles also the breathing rate is affected by sounds (52). Mangold seems to have been the first to get sound responses from a lizard: the note of a trumpet, he reported, caused quickened breathing and hissing in *Tropidonotus* (635).

The cochlea, the organ of hearing in mammals, is still imperfectly developed in birds. But if we grant that animals which produce sounds are probably able to hear them, some birds at least must be able to make pitch discriminations of wide range and great acuteness. The powers of imitation so often evidenced in bird song are proof that this is the case.¹ Lashley (574) found that a parrot reproduced the pitch of thirteen single tones whistled to it, differing from one another by full-tone intervals, with a frequency far too great to be due to chance. Craig (210) has carefully studied the responses of pigeons to a wide variety of their own sounds. Wada (1022) adopts the odd method of noting what tones will arouse pigeons from a state of "hypnosis," produced by laying them on their backs, or, to a less degree, by laying them on their sides. The lower limit was e^2 ; the upper a^3 or a^4 ; the maximal reaction was between a^2 and e^3 . The tones were whistle tones, and Jellinek (492), repeating the experiments, proved that the response was made to tone, by showing that it was not given when only the "rush of air" noise from the whistle was produced. Experiments on the association of one tone with a food compartment and another with a punishment compartment demonstrated that two pigeons could distinguish a_3 from d_4 , b_3 from d_4 , c_4 from d_4 , and c_4 from d_4 ; and one the octave e_2 - e_3 . These discriminations, as well as the responses in "hypnosis," were unaffected by operative removal of the ear drum and the columella.

Extremely significant are Hunter's (482, 483) experiments on the hearing ability of the white rat. Their net result

¹ Interesting evidence of this power in a bird which might not have been supposed to possess it was obtained by Conradi, who found that English sparrows reared by canaries acquired recognizable bits of the canary song (192).

is that these animals can hear only noises, not tones. None of the rats he tested was able to hear a tuning fork tone; the evidence is that they were unable, under the stimulus of both punishment and reward, to learn to turn to the right when the tone was sounded and to the left when it was not sounded. They could perfectly well acquire such a habit when the noise of clapping the hands was substituted for the tone. They could not form the habit when two forks of different pitch were sounded together as a signal to turn to the right. They acquired the habit of making the proper response when the tones of a whistle were substituted for the fork tones, but it was clear that they were really responding to the noise of the rush of air through the whistle, for they would react equally well when this noise was substituted for the actual blowing of the whistle. Moreover, they broke down in their choices when the whistle was sounded in another room, although they were not disturbed by the mere diminution of intensity in the sound of the whistle sounded near at hand; the natural inference is that removing the whistle to a distance made the noise accompanying its tone inaudible. In short, there seemed to be, for these rats, no difference between the sound of a pure tone and entire silence. Confirmatory results appear in Barber's (28) experiments on the white rat's ability to localize sounds: noises, such as those made by tapping on wood, were localized within an average limit of error of from two to four inches, but tuning-fork and organ-pipe tones were wholly ignored. Hunter (484) has more recently studied the rat's capacity to discriminate noises. The animals were trained first, to run right for hand-claps and left for silence; second, to turn left for the sound of a buzzer and right for silence; third, to run right for hand-claps and left for the buzzer. After this training, it was found the rats readily substituted for (that is, did not distinguish from) the buzzer sound, hissing through the teeth and the "rush of air" sound of a toneless whistle: these were all continuous noises. The noise of a metronome at 120 and at 176 could be substituted

for the hand-claps; these were intermittent noises; hence it may be concluded that the rats can distinguish continuous from intermittent noise. A metronome at 200 could not be distinguished from a continuous noise.

The experiments of Johnson (517) on the dog's ability to discriminate tones and noises gave results very similar to those of Hunter on the rat, and furnish an illuminating commentary on certain difficulties in experimentation on animals. Zeliony (1132), working by the salivary reflex method described on page 57, had reached the conclusion that the dog can discriminate between tones whose pitch differs by only a quarter of a tone. Kalischer (524), whose interest lay in testing the work of Munk¹ on the localization of the central terminations of the sensory pathways for tone in the temporal region of the cortex, succeeded in training dogs, with and without temporal lobes, to snap for food when one tone was sounded and inhibit reaction when a tone of considerably different pitch was given. Rothmann (881) and Swift (950) also observed discrimination of tones in the dog, and Kalischer (524) claims for the dog memory of absolute pitch. But the experiments of all these investigators, including those who used Pawlow's method, suffer from the fatal defect that the experimenter was in the room with the animal tested, and hence might have presented other clues, by making slight involuntary movements, which could act instead of the tones to guide the animal's choices. How serious this objection is appears from Johnson's own results. His dog subjects all learned to discriminate between a tone of 256 double vibrations and one of 384 double vibrations, an interval of a fifth, whether the tones were sounded on tuning forks or on a wind apparatus (the Stern tone variator); and to discriminate between a chord containing one of these tones and a chord containing the other tone. This was when the experimenter remained in the room. Experiments by a much more accurate apparatus, where electrically driven forks were sounded from an-

¹ Munk, H., 1890. Ueber die Funktion der Grosshirnrinde. Berlin.

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other room, while the experimenter observed the dog also from an adjoining room, the tones being sounded with exactly the same duration, gave precisely opposite results: the dogs could not discriminate. (The test of discrimination was learning to turn to the right when one tone was sounded and to the left when the other tone was sounded). Moreover, they could not even learn to take one turning when a tone was given and the other when no tone at all was given; apparently if they heard the tone at all they paid no attention to it. On the other hand, the noises of two electric buzzers, of different intensity, pitch, and timbre, were readily discriminated and localized by the dogs.¹

The same objection, that secondary clues derived from the presence of the operator may account for the seeming discrimination of sounds, applies to the work of Shepherd on cats (924, 925) and raccoons (923). The apparent fact that certain mammals are deaf to tones, while perfectly able to hear noises may, as Johnson suggests, be connected with the fact that even human beings cannot localize pure tones with any accuracy: a sound stimulus, to have practical significance, must be capable of being localized. Zeliony (1132) trained a cat to come from one room into another when a C¹ whistle was blown, and thought he had evidence of the cat's ability to distinguish the sound of this whistle from that of others differing not more than a half-tone; but the difference reacted to may have been in the accompanying noises. Hahn (379) finds the bat very sensitive to high-pitched sounds, but not to low ones.

The most striking fact about hearing in mammals seems to be that many of them can hear noises but are deaf to tones.

¹ Anrep (10a) has written in defense of Zeliony's procedure.

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CHAPTER VII

SENSORY DISCRIMINATION: VISION

§ 38. *Change of Light Intensity as a Stimulus*

IN this chapter we shall omit all reference to the function of vision as a spatial sense, that is, as giving rise to perceptions of form, size, distance, and direction.

It appears that light may act upon living beings either as a continuous or as an interrupted stimulus. That is, light maintained steadily at a constant intensity produces responses in organisms, and there are also reactions when the intensity of the light is suddenly altered, in the direction either of brightening or of darkening. Most physical forces act as stimuli only when they change in some way: an unchanging environment fails to call forth response. We may briefly survey the facts which point to the existence in animals of reactions to changes in light intensity.

Among the Protozoa, Amœba, when subjected to such changes, checks its movement at the point where the light falls. This is just what happens when a mechanical stimulus is applied, and offers no evidence of a specific light sensation (512). Folger (306) in a careful quantitative study of the reaction time to light, the stimulation period (the shortest possible duration of the stimulus required to produce response), and the latent period (the difference between the reaction time and the stimulation time), finds these processes so similar for light and mechanical shock as stimuli that he concludes the action of light on Amœba not to be photochemical at all. Schaeffer (899) reports the curious and thus far unexplained fact that Amœba can "sense" a beam of light

20 microns (thousandths of a millimeter) in diameter when they are from 100 to 120 microns distant, moving towards it.

Various ciliate and flagellate Protozoa give their ordinary negative or avoiding reaction to changes in light intensity; some of them make it on passing from a region of less to one of greater illumination, and thus "seek" the darker regions, while others give it when undergoing a change in the reverse direction, and thus tend to remain in lighter regions.

But if nothing distinguishes the negative reaction to photic stimuli from the negative reaction to any other stimulus, then nothing shows the existence of a sensation quality peculiar to the effect of light—unless a special receptive apparatus can be demonstrated. In a flagellate Protozoön called *Euglena*, a pigment spot exists near the anterior end. Now although pigment apparently is not, as Hesse (447) has emphasized, a necessary constituent of visual organs, yet its occurrence always suggests some relation to light, as it is essentially a kind of matter having the property of absorbing light. *Euglena* gives the negative reaction on entering a shadow. Is its pigment spot really an "eye spot" and concerned in this response? Apparently the reaction occurs before the pigment spot has entered the shadow, and as soon as the transparent tip lying in front of the pigment spot has been pushed into the shaded region (276). It is uncertain, then, what the function of the pigment spot is. But in another organism, which is structurally intermediate between the single-celled and the many-celled forms, pigment spots do play a rôle in light reactions. This organism is called *Volvox*, and it is really a colony of globular protozoa, each with an "eye spot." Very weak light has no effect on the movements of *Volvox*; moderate light causes movement toward the source of light, and very strong light causes movement away from the source (458). Accurate observation of these movements indicates that the eye spots are essential to them; each individual responds to a change of illumination of its eye spot (644). This much evidence, then, we have that if *Volvox* possesses conscious

Euglena
avoiding
movement
anterior

ness, changes of light intensity produce in it a specific sensation.

Among cœlenterates, response to changes of light intensity is found, although in the hydroid colonies of Tubularia it appears to be wholly lacking (776). Many sea-anemones are wholly unaffected by light stimulation, *Sagartia luciae* and *Metridium*, for example (387). Many others have been observed to contract when the light intensity is increased (361, 508, 721). *Eloactis producta* expands its tentacles only in light of low intensity, taking about fifteen minutes to do so when covered with a hood, and retracting in five minutes when the light is restored. This retraction is decidedly slower than that produced by mechanical stimulation (387); thus we have some evidence that it is accompanied by a specific sensation quality. That the responses to light are more marked in animals which have been living in comparative darkness than in those taken from illuminated spots, has been shown both for sea-anemones and for *Hydra* (304).

sea
anem

Many jellyfish also react to light more slowly than to other forms of stimulation. It is true that on *Sarsia*, a form tested by Romanes many years ago, light seemed to act as quickly as any other stimulus. If a flash of light were allowed to fall on the animal while it was moving about, "prolonged swimming movements" ensued; if it were at rest, it gave only a single contraction—another instance of the effect of physiological condition upon reaction. Sudden darkening produced no reaction, whence Romanes concluded that "it is the light *per se* and not the sudden nature of the transition from darkness to light which in the former experiment acted as the stimulus." There are, however, as we shall see, other animals in which an increase of illumination brings about response where a decrease fails, and *vice versa*. When a beam of light was thrown into a bell-jar containing many *Sarsia* and placed in a dark room, "they crowded into the path of the beam and were most numerous at that side of the jar which was nearest the light." "There can thus," concludes Romanes, "be no

Jelly

doubt about Sarsia possessing a visual sense" (873, p. 41). But as these reactions are not differentiated in any way, they cannot be taken as evidence of a specific sense, unless indeed they depend on a specialized sensory structure. This latter Romanes found to be the case; Sarsia has pigment spots on the margin of its bell, and its response to light ceased when these were destroyed. Tiaropsis, another jellyfish studied by the same observer, gave further evidence of "a visual sense" in the fact that it responded to light more slowly than to mechanical stimulation. In Gonionemus, both difference in reaction time and dependence of response on a special organ indicate that light may produce a specific sensation, always granting the presence of consciousness. Yerkes found that this jellyfish, unlike Sarsia, reacts in the same manner in passing either from sunlight to shadow or the reverse. In both cases it stops swimming and sinks to the bottom. A sudden change of illumination, therefore, checks its activity. On the other hand, if when the light falls upon it the animal is at rest, it becomes active again; but sudden decrease of illumination has no effect upon the resting animal. The inhibitory effect of strong light falling upon the jellyfish while in motion Yerkes explains as a special adaptation. For one case of such increase of illumination occurs when the animal swims, bell upward, to the surface on being disturbed; the light of the surface is of course normally stronger than that in the lower regions. The inhibition of activity resulting causes the animal, after turning over, to sink slowly, bell downward, with expanded tentacles. This is a position that gives it a better chance of catching food and carrying it to the lips than is offered by the right-side-up posture, where food would have to be carried downward against the upward current occasioned by the sinking of the animal. Light is not the only factor in producing the inversion at the surface, however, for it will occur in darkness. When swimming, Gonionemus moves toward the light if the latter is fairly intense, but comes to rest in the shaded portions of the vessel containing it. The

reaction time to light is much slower than that to other stimuli, but the animal responds most promptly when certain pigmented bodies at the base of the tentacles are exposed to the stimulus. If the margin of the bell containing these bodies is cut off, no reaction to light can be obtained (1095, 1102, 1118). A great variety of structures apparently sensory in function is found on the bell margin of different genera and species of jellyfish. Some of them are statocysts. Others suggest a visual function, and in the Cubomedusæ there are fairly well developed eyes.

Various annelids show response to changes in light intensity, the leech *Clepsine*, for example: the slightest shadow cast on the surface of the water in a dish where these animals are resting quietly will cause them to reach up and sway from side to side in an apparent search for prey (1071). On the other hand Gee (348) says of the leech *Dina microstoma* that the casting of a shadow on it makes it contract. This is apparently the more primitive and the more common type of response to a change in light intensity. *Dina* contracts in just the same way when mechanically jarred, but a difference in the physiological process involved is indicated by the fact that these leeches get used to repeated shadows, and cease to respond, much more quickly than they get used to repeated jars. When the earthworm has partially emerged from its burrow, and has its tail still inserted, a flash of light will produce quick withdrawal into the burrow (229, 453), but the reaction time to light is much longer than that to mechanical stimulation. The part of the earthworm's body affected by the light also influences the reaction. Darwin indeed reported that the worms withdrew into their burrows only when light fell on the head end (229), but decapitated worms were found by Graber to respond to light like normal ones, only less strikingly (361), and Yung (1126) obtained evidence that sensitiveness to light is distributed over the body. According to Hesse the anterior end of the worm is most sensitive, the tail next, and the middle region least (440). Not only

the region, but the amount of body surface affected, makes a difference. When the whole length of the worm was illuminated, the percentage of reactions was to that obtained where the front third only was involved as 26 to 10.2, while the relative occurrence of responses where the middle third and the posterior third alone were stimulated is represented by the figures 2.4 and 1 respectively (761).

W. N. Hess (439) has recently shown, in opposition to the results of Graber just quoted, that a decapitated worm does not react normally, for removal of the cerebral ganglion abolishes the negative reaction, and causes the worms to become "positive" to light of much stronger intensity than usually produces this effect. He also finds a type of cell in the earthworm which he believes to be a true photoreceptor.

In many of the marine worms well-developed eyes exist, although not such as are capable of giving clear images. Their function seems to be chiefly that of receiving stimuli from shadows. Many tube-dwelling worms will withdraw into their tubes if a shadow is cast upon them (386, 445, 885).

Turning to the mollusks, we find that the siphons of the *Acephala*, which are projected from the shell to take in currents of water containing nourishment, are withdrawn in response to sudden darkening in some cases, to sudden illumination in others, and in still other instances to either (264, 720, 885). The danger of arguing the existence of sensory discrimination from structure alone is well shown in the case of snails, for although many of them have eyes of some degree of development, these very species have been shown to be devoid of sensitiveness to light (1129, 1130).

"Skioptic" reactions, or reactions to shadows, appear among various echinoderms. The sea-urchin *Centrostephanus longispinus*, for instance, which lacks even a rudimentary eye spot, will when a sudden shadow falls upon it direct its spines towards the shaded side. The reaction time involved is decidedly longer than that to mechanical stimulation, and moreover, although pieces of the animal will react to the latter,

responses to shadows depend on keeping the system of radial nerves intact. (This observation, according to Cowles (208), does not hold for the sea-urchin *Toxopneustes*). Hence Von Uexküll, who made the above observations, concluded that a special set of nerve fibres is concerned in photic reactions (1000).

Dubois had suggested from studies on the mollusk *Pholas dactylus*, that in such cases the pigment changes which occur, under the influence of light, over the surface of the body, furnish the stimulus (264), but Von Uexküll thinks this impossible, as the light reactions occur before the pigment changes do. This migratory pigment, he believes, acts merely as a screen; the source of excitation for the optic fibres may lie in another pigment which he has extracted and found very sensitive to light (1000). *Centrostephanus*, according to Hess (426), shows pigment changes when the light is decreased by a very slight amount, just enough to be perceptible to the human eye. In certain mollusks two forms of reaction to shadows occur; one, a contraction of the body, is produced by the action of light on the skin; the other, a rearing movement, is brought about through the eyes (318).

Starfish have pigment or eye spots on the arm-tips. As a rule, they seek light: Romanes (873) and Tiedemann (971) report that the light reactions are abolished if the eye spots are removed. MacCurdy (624) finds, however, that in *Asterias forbesii* the light reactions are independent of eye spots: Cowles (209) has shown that *Echinaster* will react to light without eye spots, although some evidence of dependence on the sense organ is indicated by the fact that the response is slower; Plessner (823) holds that skin sensitivity is responsible for reactions to light intensity, and that the eye spots enable the animal to respond to the direction of the light; Cowles (208), again, observes that when pieces of starfish and sea urchins are cut off, their tentacles and suckers still move in response to the casting of a shadow.

Among crustacea, which are provided with a peculiar visual

organ, the compound eye, to be described later, the chief function of the eye seems to be that of responding to shadows and movements. Bateson, watching shrimps and prawns, noted that they apparently could not see their food when it had been taken from them and lay near at hand, but quickly raised their antennæ when an object was passed between them and the light (33). The little fairy shrimp, *Branchipus*, will stop swimming as soon as the edge of a shadow falls upon it. Skioptic reactions in the family of *Cirripedia*, to which the barnacles belong, were noted by Pouchet and Joubert in 1875, as well as the fact that those individuals which were attached to rocks, where a sudden shadow might mean danger, reacted, while those attached to floating objects, and therefore normally exposed to light fluctuations, did not (833). *Daphnia* (see p. 146 f.) reacts to moving shadows through the medium of its eyes (7).

Bozler (117) thinks that the simple eyes or ocelli of insects are concerned with responses to quick changes of light intensity: he found that such responses were much slowed when the ocelli of the fruit-fly were removed. Insects without ocelli, such as some butterflies, have to stop flying when the light is much diminished by a passing cloud. Homann (469), after determining the optical constants of the ocelli in a number of insects, believes that ocelli, which take in a good deal of light, aid the compound eyes in producing tropic (see p. 133) reactions in faint light, but Bozler reports that the threshold for phototropism is the same even when the ocelli are removed.

Among the vertebrates, where for the most part we find good image-forming eyes, specialized responses to movements and to changes in light-intensity give place to reactions involving a more or less adequate image of the stimulus object. Amphioxus, however, the most primitive existing vertebrate, reacts through the skin only. Its responses to light offer as chief evidence that they are accompanied by a specific sensation quality the fact that they may be fatigued independently of other reactions. The only structures suggesting a

visual function are pigment spots on the back near the head, and other pigment spots distributed down the back. *Amphioxus* makes negative responses to light, especially when the light, from which heat rays have been extracted by passing it through water, is directed at any point on the back, the most sensitive region lying just behind the eye-spot (558, 749). Fatiguing the light reactions had no effect on response to other forms of stimulation (749).

True skin sensitiveness to light has been observed in larval lampreys, which will give negative reactions even when the optic nerves are cut (746), and in cave-dwelling blind fish (272). Parker, however, finds no other fish in which it exists, although it is quite common in amphibians. He therefore reaches the conclusion that in vertebrates, skin sensitiveness is not a primitive form of visual sensibility, from which vision by the eye has been derived, but a "secondarily acquired peculiarity." He points out that the fish and amphibians which show it are freshwater animals, whereas the primitive vertebrates were certainly marine (751).

As we have seen, the most primitive type of reaction to a sudden change of light intensity is the checking or inhibiting of the animal's movements. This type of reaction is called by Loeb "*sensibility to difference*." In many cases its relative slowness, as compared with similar reactions to other stimuli, or its dependence on a special organ or region of the body, gives evidence that it is accompanied by a specific sensation quality.

§ 39. *The Continuous Action of Light: Photokinesis*

When light stimulates not through its change of intensity, but through its action as a constant force, its effects are apparently of two kinds. One of these is the phenomenon which Loeb (599) calls the tropism, from the Greek word meaning "to turn." In the tropism, the organism takes up a definite position with reference to the action of a force. The phenomenon is therefore connected rather with the spatial

aspect of the sense of sight than with its qualitative aspect, and we shall consider it in a later chapter. The other type of effect caused by light as a constant stimulus is that it stimulates or inhibits the general activities of the animal. Thus some animals are restless in strong light, others in darkness. As a result of this influence, the former tend to form collections in the dark, where they remain quietly; the latter in the light. This influence of a certain intensity of light to stimulate to activity we may call its *kinetic* effect, or *photokinesis*. The cœlenterate Hydra, for example, has a disposition to come to rest in the more illuminated parts of the vessel containing it (980, 1077). Very strong light, however, makes it wander about until it happens to reach a more shaded region. Thus if the animal is subjected to light either above or below a certain "optimum" of intensity, it is restless. A vague uneasiness is the kind of psychic accompaniment to this behavior most naturally suggested. Since repeated strong mechanical stimulation also will make the animal wander, nothing points to the existence of a specific visual quality in this consciousness.

The medusa *Gonionemus* is less active in darkness than in light, and comes to rest in darkened regions, where it thus tends to collect (1095): such collections are evidently not due to "choice" on the animal's part. Planarians are more active in light (29, 591, 595, 441): if decapitated and hence eyeless, their reactions are slower (598). In land isopods (crustacea), continuous light produces both a kinetic and a directing or tropic effect (1); the same is true of the whip-tail scorpion (771), and of the mollusk *Balanoglossus* (216). Photokinetic effects seem to be common among insects, many of which, the house fly, for example, the mason wasp (993), and the honey bee (686), are active in light and sluggish in darkness. These animals are naturally so much more active than Hydra and planarians that we do not find them forming collections in the regions where they can rest: they seem able to continue in rapid motion for long periods, and it is

rather a pleasurable than an uneasy activity that is suggested by the aerial dances of insects in the sun.

Tadpoles, of course, have no eyes. At an early stage of their development they show photokinesis, the effect being produced through skin nerves: later a definite orientation to light makes its appearance (190).

§ 40. *The Problem of Color Vision*

The question as to whether a given animal has the power to discriminate between colors as colors is much more complicated than any other problem connected with the sensory discrimination of animals. Its difficulty is due largely to the peculiar relations existing between the intensity and the wave-length of light as regards their effect on the eye. Generally speaking, of course, the intensity of white light determines the brightness of the grey or white sensation experienced by the human eye; the intensity of colored light determines the brightness of the color, and the wave-length determines the quality of the color. Upon a totally color blind human eye wave-length as such has no effect, but different colored lights may by their different intensities produce sensations of different brightness; in this case different greys. Reasoning by analogy, it appears that when an animal distinguishes between two lights of different wave-length, unless they are known to be of the same intensity, it may be basing the discrimination on intensity differences, and may be seeing greys in place of colors. The situation becomes still more complex when we realize that we must distinguish between the physical and the physiological intensity of a light stimulus. Two lights of different wave-lengths may have equal intensity as physical forces, but owing to the constitution of the visual apparatus one of them may produce more effect through the eye than the other does. For example, in sunlight there is a greater quantity of yellow rays than of other wave-lengths; in gas-light a greater quantity of yellowish-orange. If we show to a

person with normal color vision, in a good light, the band of spectral colors, he sees the yellow region as the most intense, the brightest region. If, however, we show the spectrum to a totally color-blind person, he sees it not as colored but as a band of different greys, and the brightest grey is not in the yellow region, but in the yellow-green. Some peculiarity of his retina intensifies the effect of the yellow-green rays: their physical intensity is the same, but their physiological intensity is different. As a result of shifting the physiological intensity towards the violet end of the spectrum, the totally color-blind person sees red as a grey much darker than the brightness of red to the normal eye would lead one to expect. To add to the complexity of the situation, this altered distribution of physiological intensity holds also for the normal human eye in very faint light: we are all totally color-blind in twilight. In the human eye, the apparatus responsible for the shift of intensity appears to be the retinal rods, which function more than the cones in faint light, and which may be the only visual apparatus functioning in the totally color-blind eye.

These complex relations being recognized, we cannot attack the problem of color-vision in animals by merely showing an animal two different colors and proving that he reacts, or can be trained to react, differently to them. For even if he were totally color-blind, he would probably still see them as different, only they would be different shades of grey. To meet this difficulty, various experimental methods have been devised, which we shall proceed to survey.

§ 41. *Methods of Investigating Color Vision: I. Methods Based on the Distribution of Physiological Intensity in the Spectrum*

The assumption involved in these methods is as follows. If the most effective region, at ordinary light intensities, for a given animal is the yellow region, which is also the most effec-

tive region for the normal human eye, then the animal can see colors. If the most effective region at ordinary light intensity for a given animal is the yellow-green region, which is the most effective region for the totally color-blind human eye, then the animal is totally color-blind. The mere statement of this assumption arouses skepticism: how can we infer from human to animal vision, especially invertebrate vision? Nevertheless many investigations have relied on such an inference, and we must proceed to survey them. How can we find out which region of the spectrum is most effective, has most physiological intensity, for a given animal?

(a) We may observe the effect of different spectral regions on the animal's movements of locomotion.

For example, if the organism has a tendency either to seek or to avoid light, the effectiveness of differently colored lights may be directly compared. This has been done for microscopic animals by an arrangement such that two beams of light fall on the organism at right angles to each other. If the animal either seeks or avoids light, and if the two beams are of equal objective intensity, the animal will move on a diagonal between them. If one ray is either objectively stronger than the other, or has a stronger physiological effect, the course of an animal which seeks light will be inclined towards the more effective beam; that of an animal which avoids light, towards the less effective beam. If, now, the two beams are of equal objective intensity but different wave-length, it will be possible by observing the animal's course to determine the physiological effectiveness of different colors. Mast (654), using this method, found that some animal forms, such as the larvae of the blowfly, are most strongly stimulated by that region of the spectrum which acts most strongly on the color-blind human being; others, such as the earthworm and the larvae of the worm Arenicola, are most responsive to blue, as plants are. We shall note later the significance which Loeb ascribes to resemblance between plant and animal responses to light.

color-blindness
Serpula
fish
 Hess (427) inferred the total color-blindness of the marine worm *Serpula* from the fact that when tested by the direction in which it turned when subjected to light passing through differently colored glass, it showed evidence that the yellow-green had most effect, and that effectiveness diminished rapidly towards the red end of the spectrum and slowly towards the violet; the distribution of effectiveness being like that in the color-blind human eye. He finds that the feet of starfish belonging to the *Astropectinidae* are very sensitive to light: red light has little effect on them; blue-green light, even when much darker than red to normal human vision, decidedly more effect, as would be the case also on the color-blind human retina. The same results appear in the sea-urchin (426). For the caterpillars of *Vanessa urticae* the effectiveness of colors in determining locomotion is that for the color-blind human eye (434).

Daphnia
 Studying the movements of the eyes of the little crustacean *Daphnia* (Fig. 10, page 147), Hess (419) noted the effect on them of increasing and of diminishing light intensity; then, keeping intensity constant, he varied the wave lengths, and found that the "darkening" movement was made when the light was shifted from yellow-green either to blue or to red, but most decidedly in the latter case. In a later paper (433), he observes the distribution of spectral effectiveness in *Daphnia* and some of its near relatives by another method. When these animals are adapted to light, any slight darkening slows their movements and they tend to sink in the water; any slight brightening speeds them up and they rise again. Thus one needs only to note what colored rays produce a sinking. The distribution of effectiveness found was again that for the color-blind human eye.

The same observer (425, 428), using colored lights of measured intensities, studied their effect in causing bees to collect under them; again the relative effectiveness conformed to the color-blind human type. He reports similar results with butterflies, and finds that the spectrum is seen by fish with the

same distribution of brightness characteristic of human color-blindness; whence he concludes, in opposition to all other authorities, that fish are color-blind like invertebrates (517, 421).

Amoeba, as we have seen, has no phototropism, but reacts to a change of light intensity by a checking of movement at the point affected. When tested by light passed through differently colored filters, the majority of individuals react most decidedly to blue, although some show most definite response to violet, others to green or yellow, and still others to red (647). Schmid (903) says that red and yellow affect the sea-anemone *Cereactis aurantiaca* differently from green and blue, but does not state wherein the difference consists.

(b) Another way of determining the relative effectiveness of different colors is possible in the case of animals whose eyes have contractile pupils: since the pupil grows smaller, the greater the effective intensity of the light, if colored lights of equal objective intensity are used, that one which causes the greatest degree of pupillar contraction will be physiologically the most effective. Hess has devised an instrument for measuring the amount of pupillar contraction, using spectral lights and white lights of controlled intensity; and for cephalopod mollusks finds that yellow and green rays produce more effect than do red and violet rays; hence he concludes that these animals are totally color-blind (419). His observations by this method on birds are especially interesting: for day-birds he finds yellow the most effective region, and therefore grants them color vision; for night-birds, he says the most effective rays are in the yellow-green; thus their vision, like our own faint-light vision, is totally color-blind (416). Honigsmann (470) is inclined to be skeptical about the accuracy of these pupillar measurements.

(c) Still another physiological process has been observed in the endeavor to establish the relative effectiveness of different spectral regions, but it suffers under the disadvantage of being accessible to observation only after the removal of

the eye. Light acting on the retina produces electric currents, which are called action currents, but obviously they cannot be measured by the galvanometer except on the dissected eye. The maximum current from the light-adapted retina of a frog was produced by yellow light; from the dark-adapted retina, by yellow-green light (449).

(d) The effect of different colors upon the breathing rate of the common octopus has been observed (825). The animal was placed in various colored liquids, whose actual color had been determined by the spectroscope. The number of respirations per minute was found to increase when the octopus was transferred from white to colored light; the greatest effect was produced by violet and blue, the least by red. Such a distribution of effectiveness suggests the totally color-blind human retina. The same investigator found that with fish the most rapid breathing occurred under red stimulation, and explains this by suggesting that in the normal habitat fish are adapted to blue and violet rays (826). Clearly, here, in the possibility that an animal's environment under natural conditions determines the effectiveness of different spectral regions, we have a new factor in the already complicated situation. Breathing rate, in any case, seems likely to be determined by the emotional effect of a stimulus, and thus to be untrustworthy as an index of the purely sensory effect. Fish, for example, may be frightened by red light, although they see it as no brighter than any other color.

In connection with the problem of the effectiveness as stimuli of the different spectral regions, we cannot avoid considering the ultra-violet rays. These do not cause visual sensations when they act on the human eye. Graber (361) in 1883 attempted to test the color discriminations of a number of animal forms by observing their preferences for differently colored lights. In the case of the earthworm, it was found that if a choice was offered between a dark compartment and one illuminated by diffuse daylight, the number of individuals found in the dark at the end of an hour was

on the average 5.2 as many as those in the light; and considerable preference was shown even for a compartment lighted through ground glass as compared to one with full daylight intensity. When colored glasses were placed over the compartments, the worms were found to prefer red to blue even when the latter was much darker than the former to the human eye; green to blue under similar conditions, and red to green; and they emphatically preferred white light from which the ultra-violet rays had been extracted by a suitable screen, to ordinary white light. It may well be that the effectiveness of blue in determining avoidance is due to the ultra-violet rays found in blue light. In the case of Daphnia the evidence as to the action of ultra-violet rays is conflicting. Lubbock (612) found that these normally positively phototropic animals seek a region affected only by the ultra-violet rays, in preference to darkness, although the two look alike to our eyes. On the other hand, Loeb (597) and Moore (696) report that the action of ultra-violet rays instantly makes Daphnia avoid the light containing them, and that individuals without eyes are unaffected by these rays; so that they must act on the eye of these crustaceans, although not on the human eye. Graber (362) showed that positively phototropic insects prefer colors containing the ultra-violet rays, while negatively phototropic ones prefer red, from which these rays are absent. Similar observations were made by Lubbock on ants, which in their underground life are negatively phototropic, the eggs and larvæ apparently needing darkness in order to develop; but on their foraging expeditions are comparatively indifferent to light. They showed a preference for red when tested, and a tendency to avoid the ultra-violet rays, so marked that they preferred to leave their eggs under bright daylight from which these rays had been extracted by chemical screens, rather than in darkness that contained ultra-violet rays (609, pp. 207 ff). Graber suggested that these rays produce a skin-sensation in the ants; but Forel agrees with Lubbock that the effect is visual, because he found that var-

nishing the eyes made the ants indifferent to ultra-violet (308). Ants of the family Lasius seem to be normally indifferent to these rays (312). It is just possible, then, that a visual sensation of quality wholly unknown to our experience may accompany the action of ultra-violet rays on insects. Schiemenz (902) and Wolff (1085) report that fish get such a sensation from ultra-violet. Loeb (585) has noted that the effect of violet and ultra-violet rays, as compared with that of the rest of the spectrum, is greater, the less developed the visual organ. Termites, which seek darkness, prefer red to blue colored glass (10). Lubbock (609) observed that bees which had eaten honey from blue paper would pick out the blue pieces from a number of differently colored papers, whose positions were altered during the experiment. Forel (308) got similar results, and reports that a bumble-bee thus trained selected all the blue objects in the room for special examination. Now Hess (438), after finding that caterpillars, bees, daphnias, ants, butterflies, Chironomas larvæ, and moths can distinguish between two colorless lights of equal brightness, if one has ultra-violet rays and the other has not; and that the sensitiveness of these arthropods to ultra-violet extends very far out beyond the violet end, a fact which he refers to the effect of fluorescence in the refracting parts of the compound eye, maintains that all these special reactions to blue are reactions to ultra-violet, and have nothing to do with color vision (436). As we shall see, however, this argument is refuted by the experiments of von Frisch and Kühn.

We may note the following objections to the general method of concluding color vision or color blindness in an animal from the degree in which it reacts to the various spectral colors. First, it is not strictly safe to infer that an animal is color-blind because it shows the same distribution of effectiveness of spectral colors that is characteristic of the color-blind human being. Particularly is this inference dangerous in the case of invertebrate animals, whose retinal substances may be quite unlike those of man. Secondly, when an animal,

for instance, the octopus, shows great sensitiveness to the violet end of the spectrum, we need not conclude that it is totally color-blind; it may be unusually sensitive to ultra-violet rays. These rays, which are distributed to a certain extent through the visible violet and blue regions of the spectrum, may exert an irritating effect on certain animals, analogous to their effect on human skin; and such an effect, rather than any visual process, may be responsible for the animal's behavior. Thirdly, the adaptation of the animal to the colors of its normal environment may render it especially sensitive to other colors.

It must be remembered that in all experiments by this method in any of its forms, the objective intensities of the differently colored lights should be the same. The aim is to study the distribution of physiological intensities, and thence to conclude the nature of the animal's retina.

End Lect.

§ 42. Methods of Investigating Color Vision: II. Methods Based on Independent Variability of Reactions to Intensity and to Wave Length.

The chief source of error in experiments designed to show that animals can discriminate colors as such being the possibility that colored light may act only through its intensity, physical or physiological, rather than through its wavelength, an obvious way of eliminating this possibility will be to show that an animal's reactions to color vary independently of its reactions to the intensity of the light. Experiments by this general method may conveniently be divided into those which employ innate and those which employ acquired reactions of the animal.

1. Independent variability of innate reactions to intensity and to wave length.

(a) Action currents. A study of the electric currents generated by the action of light on the eyes of day and night birds gives evidence, confirming that from the pupillar re-

flex, that night birds are color-blind. In the day birds, each color gives a characteristic deflection of the galvanometer, not due to its intensity; while no such deflections appear for the night birds (555).

(b) Breathing rate. It is often possible to observe and count the breathing movements of an animal. By fastening a suitable "harness" about the thorax of a vertebrate animal and connecting it with a recording instrument, the breathing may be registered. Babak (19) has studied the effect of different colors on the frog's breathing; its rate and the movements involved in "throat" and "lung" breathing. The fore-brains of the animals had been removed, a proceeding which makes the breathing of the resting animal more regular. He found that each color produced a breathing curve of a certain specific pattern, and concluded that the colors have specific effects on the eye, independent of their intensity. Rouse (883) observed that differently colored lights had on the average different effects in quickening the rate of breathing in the pigeon.

(c) Skin color changes. Various flatfish change their markings and colors to match the ground on which they lie. Von Frisch (319) investigated this phenomenon in the fish *Phoxinus laevis*. If two individuals whose skins are, at the time, of equal brightness, are placed one on a yellow ground, the other on a grey ground, and these grounds are properly chosen as to brightness, the fish will remain unaltered in brightness, although if either ground is made lighter or darker, a corresponding change appears in the skin of the fish lying on the altered ground. When the fish remain at the same brightness, then, it may be inferred that the effective intensities of the yellow and the grey are identical. But after a few hours, it will be found that the fish on a yellow ground shows a yellow stripe which does not appear on the other fish (see also 375). Mast (655) has made a very thorough study of this phenomenon in the flounders *Paralichthys* and *Ancyclopsetta*. These fishes become strikingly bluish on blue

grounds, greenish on green grounds, and so forth, adapting themselves to blue, green, yellow, orange, pink, and brown, and less successfully to red. The color changes are brought about by certain pigment-controlling mechanisms in the skin, which are connected with the sympathetic nervous system. But the color stimulus acts through its effect on the eyes: the changes do not occur if the eyes are covered.

Watson (1051) does not think that these observations prove color discrimination in the fish. He says, "Ordinarily we mean when we say that an animal is sensitive to difference in wave-length that such stimuli play a rôle in the adjustment of the animal to food, sexual objects, shelter, escape from enemies, etc.; i.e., that such stimuli initiate activity in arcs which end in the striped muscles." Because the changes of color are produced not by such arcs, but by the sympathetic nervous system, Watson thinks color vision not proved: "we can easily conceive," he says, "of mimicry of this kind taking place in an animal whose retina does not contain the physico-chemical substances necessary to initiate response to differences in wave-length." But since the changes of color are induced by differences in wave-length and induced through the retina, we may reply that it does not seem easy, or in fact at all possible, to conceive the absence of such photochemical substances from the fish's retina. Moreover, Mast found that fish which had thus become adapted to a given color will seek that color: this is an activity involving the striped muscles.

Schnurmann (907) comes to the rescue of Hess's cherished conviction that fish are color-blind. He finds that these fish, when kept in the dark, acquire yellow coloring, and explains the situation by maintaining that a certain yellow pigment in the fish's retina is responsible. When this pigment absorbs light, which of course would be only short-waved light, the yellow pigment cells of the fish's skin contract. When the retinal pigment does not absorb light, which is the case in darkness or when it is on a yellow ground, the yellow pigment

cells of the skin expand and yellow color appears on the skin: the whole affair has nothing to do with visual sensation. Von Frisch (334) offers in rebuttal experiments where a very dark grey ground was used, on which the retinal pigment would have little chance to absorb light, and a yellow ground so unsaturated that it reflected considerable short-waved light, thus offering much chance of absorption to the retinal yellow pigment. Contrary to Schnurmann's theory, yellow skin color appeared on the yellow but not on the grey ground.

(d) Choice. There are a number of researches on the tendency of animals to choose certain colors rather than others, in which the question arises whether the choice is determined by wave-length or by intensity, and where this question has ultimately been answered by showing that intensity could be altered without changing the response, which must therefore have been determined by wave-length; or with resultant alteration of response, which must therefore have been determined by intensity. Bert (56), in 1869 used an electric-light spectrum thrown on a vessel containing small crustacea whose ordinary response to light was strongly positive; and found that the animals "chose" the yellow-green regions; this result was confirmed when he allowed each color to act separately through a narrow opening and noted the speed of the positive reaction produced. He suggested that this preference might not be a matter of color-vision, but of response to the greater intensity of light in the yellow-green region; and Merejowsky proved that such was the case by showing that certain crustacean larvæ, those of *Balanus* and *Dias longiremis*, manifested no color preference when the colored rays were made of equal intensity (674). In 1883 Sir John Lubbock (610, 611) had a sunlight spectrum thrown on a trough containing Daphnias, tiny crustacea of the lowest subclass (Fig. 10), which are strongly positive when light-adapted. At the end of ten minutes glass partitions were slipped across the trough at the approximate dividing lines between the colors, and the number of animals in each compartment was

counted. The greatest number was repeatedly found in the yellow-green section. Lubbock attempted to prove that this choice was based on color rather than intensity by various modifications of the experiment, but without entirely conclusive results (612, pp. 221ff.). And Yerkes in 1900 (1092), working on Simocephalus, a close relative of Daphnia, found that when a gaslight spectrum was used, the animals collected in the red-yellow region, that of greatest intensity for such light; while if this region had its intensity diminished by a screen of India ink or paraffin paper, the crustaceans moved out of it. All of this seems to argue



FIG. 10.—Daphnia. *at*, antenna; *atl*, antennule; *oc*, eye. After Yerkes.

against reactions to color in the animals concerned. Nevertheless von Frisch, who believes as strongly in the color-vision of some invertebrates as Hess denies it to all of them, presents some evidence to support his view in the case of Daphnia. When Daphnias have been kept for some time in light of a certain intensity, an increase in the intensity makes them avoid light, while a decrease makes them seek it. But if a blue screen is interposed between the light and the animal, in spite of the fact that the intensity is thereby diminished, the Daphnias avoid it; if yellow light is added to white light, in spite of the fact that the intensity of the light is thereby increased, the Daphnias seek it (336).

Ewald (289) reported that of the Daphnias under his observation one group sought the light, which was in this case most effective in the yellow-green regions; while another group avoided light, and for these the most effective region in determining avoidance was the blue-violet, so that the ef-

fect of colored rays was independent of their intensity. And O. Koehler (546) has recently offered evidence for color-vision in Daphnia. He states that when dark-adapted they are totally color-blind, like ourselves, but that when light-adapted they see two color-qualities, one produced by long-waved light from red to green, and one by short-waved light from blue to purple. The evidence is as follows. Individuals which are so adapted to a moderate intensity of colorless light that if it darkens they become positive, if it brightens, negative, are positive to light from red to green and negative to light from blue to violet, no matter whether these produce brightening or darkening.

Minkiewicz also is a partisan of invertebrate color-vision. He observed that he could alter the reactions of a Nemertean worm, Lineus ruber, to colored light, while its response to white light remained unchanged. When placed in dilute sea-water, the animal would, after a day, direct itself toward violet rays although still negative in response to white light. On the fourth day the ordinary "chromotropism" returned; that is, the worm sought red light. After two or three weeks of life in the diluted sea-water the worm again showed inverted chromotropism, becoming positive to the violet rays while still negative to white light. Intermediate stages in the passage from the red- to the violet-seeking phase were also observed (683). Hess rejects these observations (437). Certain crabs are thought by Minkiewicz to give evidence of color vision. The hermit crab is naturally attracted to light, but when subjected to colored lights it does not seek them in the order of their intensity. Green is the most attractive color, violet next; then the order is blue, yellow, red, and black (684, 685). He finds it possible with crabs also to reverse the response to white light without affecting the response to color (683).

(e) Differential fatigue. An ingenious attack on the problem of color vision has been made by W. F. Hamilton (383), using the common fruit-fly as subject. The insects were in a

state of adaptation to darkness. Two beams of monochromatic light, of controlled intensities, were thrown one into each end of a tubular cell containing a number of the insects, which are strongly positive in their phototropism. The intensities of the two beams were regulated so that the flies went to neither of the two ends; that is, they were made physiologically equal. When this had been done, one of the lights, called the stimulating light, was cut off, and the flies remained exposed to the other light, called the fatiguing light. The animals at first moved towards it, but after a time, as a result of sensory fatigue, the positive response was much diminished. The stimulating light was then allowed to act again, in order to observe whether fatiguing for the one light had also fatigued for the other. If the flies did not now orient and move towards the stimulating light, it might be concluded that the two lights had affected the same sense mechanism, and could not be discriminated: if the flies did orient towards the stimulating light although fatigued for the other light, it might be concluded that two different sense-mechanisms were involved and that discrimination would be possible. The results showed that if the lights were of the same or nearly the same wave-length, fatiguing for one involved fatigue for the other: if there was considerable difference in wave-length, this was not the case. When the smallest differences in wave-length which produced differential fatigue were measured, evidence was found for two receptor systems, one for the blue-violet and one for the blue-green.

2. Independent variability of acquired reactions to intensity and to wave-length.

Can an animal be *trained* to react to the color of light in a manner differing from its reaction to the intensity of light? Many investigations have been made on this problem, which offers an opportunity to study both the color discrimination and the learning capacity of the animal. The methods used may be grouped under several heads.

(a) Some of the older investigators proceeded to present

the color stimulus along with a grey which looked to the normal human eye, in daylight vision, of equal brightness with the color; the assumption being that if the animal could discriminate between the two, it possessed color vision for the color used. Kinnaman (540) showed that monkeys could pick out a tumbler covered with colored paper from among three similar tumblers covered with gray paper which appeared equally bright with the color to ordinary human vision. A more refined method of selecting the grey equivalent of a color than this method of mere inspection makes use of the phenomenon of "flicker." If a disk made of a colored and a grey paper be rotated a little too slowly to give a smooth mixture, the peculiar appearance of "flickering" will be observed if the color and the grey are not of equal brightness to the observing eye, but will disappear when a grey equally bright with the color is selected. Cole (180) concludes that raccoons have color vision by showing that they can distinguish colors from greys equated to the colors by this method. Really, however, no determination of the brightness equivalent of a color to the human eye has any bearing on the problem of color-vision in animals. If they are color-blind, their difficulty would more probably lie in distinguishing between a color and its brightness equivalent for the color-blind or dark-adapted human eye; and quite possibly the brightness (grey) which they see instead of color may be unlike the brightness-value of that color to either the light-adapted or the dark-adapted human eye.

(b) An animal may be trained to discriminate between two stimuli differing in color, and then the relative intensity of these stimuli may be greatly altered. If the animal still distinguishes between them, this fact offers evidence that they are distinguished as colors, since if they were seen as greys, there would be a total change in their brightness under such conditions. Professor Bentley and the writer (1036) trained a small brook fish, the creek chub, to bite at forceps to which red sticks were attached, and to refrain from biting

at similar forceps carrying green sticks. The fish thus trained continued to bite at red rather than green even when a red was used which to the human eye was much lighter than the green; the original red having been darker. Reighard (856) trained the grey snapper to avoid minnows dyed in certain colors and select those dyed in other colors, and showed that a given color could be identified although appearing in several brightnesses differing to the human eye. The experiments of Yerkes (1113) on the dancing mouse proved, however, that varying the intensity of a color stimulus so that it appears to the human eye greatly altered in brightness is not a sufficient precaution. His method consisted in teaching the animals to associate one of two differently illuminated compartments with an electric shock. The intensity of the illuminations could be regulated by varying the distance of the lights from the compartments. The mice could distinguish light blue from orange, green from red, violet from red, even when their brightnesses were considerably varied. Yet it seemed probable that these discriminations were based really on brightness rather than on color differences, for after a mouse had learned to choose green rather than red, on being offered a choice between light and darkness, it uniformly chose the former, although untrained mice showed no such preference. Apparently then, the green had been previously discriminated simply as the lighter of the two impressions, and to the eye of the mouse, as to that of the color-blind human being, red looks an extremely dark grey. To make valid the method of varying color intensities, the variation must occur throughout the widest possible range, as in the experiments of Lashley (573) on the domestic fowl. He used spectral light whose intensity was accurately controlled and measured by its effect in producing electric currents through a selenium cell, the Yerkes-Watson apparatus (1124). The ability of the fowl to distinguish red and green was demonstrated under the following conditions, which seem to exclude the possibility of discrimination by brightness differences: each of

the lights alternately was reduced to threshold intensity while the other remained at full intensity; white light of a constant intensity was substituted for each light in turn; each light was in turn exposed alone, one passage being left dark. By the same apparatus Watson (1048) reached the conclusion that red has but little stimulating value for the eye of the monkey. Schiemenz's (902) work on the fish *Phoxinus laevis* used spectral colors whose intensity was carefully controlled and widely varied: he got evidence for the existence of red, yellow, green, blue, violet, and ultra-violet color qualities.

Indications of color-blindness in the grey mouse were obtained by Waugh (1056), using red filters and papers: these could be distinguished from grey of equal brightness to the human eye, but the distinction tended to disappear when the red was made lighter and to increase when the red was made darker. Turner (990) infers color-vision in the honey bee from its ability to pick out objects of the same color as that on which it had recently found food, under the varying lights and shadows of an out-of-doors environment: this is probably an insufficient precaution.

(c) An animal may be trained to distinguish between two differently colored stimuli, and then its ability to distinguish between different shades of grey may be investigated. If the latter is decidedly poor, a presumption that the colored stimuli were discriminated as colors rather than as greys is established. Wolff's (1085) study of color vision in the fish *Phoxinus laevis* is an example. He used spectral colors of controlled intensities. Most individuals were more sensitive to color differences than to brightness differences. These fish have a tendency to seek the brighter of two white lights, and the brighter tones of the same color, but their ability to associate colors with different spectral regions was uninfluenced by the brightness differences between these regions. Twenty color-tones were discriminated, within the five principal qualities red, green, blue, violet, and ultra-violet. Kinnaman's monkeys (540), which had learned to identify a vessel cov-

ered with a particular colored paper as containing food, were shown to be unequal to discriminating between grey papers whose brightnesses were to the human eye the same as those of the colors. White (1070) found that mudminnows which had learned to distinguish from each other red and green, red and blue, yellow and green, all produced through colored filters and of known wave-lengths, could not learn to discriminate between photographic plates of different shades of grey. De Haan (67) who succeeded in training monkeys by the Multiple Choice Method to distinguish red, green, blue, and yellow papers from one another and from thirty different shades of grey, reports that they could not discriminate between two successive shades of the grey series. Kohts (556), who required a chimpanzee to select from a number of objects one matching in color or brightness a sample shown him, succeeded with a whole range of spectral colors, and found that differences in the brightness of the colors were oftener confused than differences in their hue; also that greys were oftener confused than colors.

(d) An animal may be trained to distinguish a lighter from a darker grey. If then we find that it fails to distinguish between one of these greys and a color, we may conclude that the grey and the color look equally bright to the animal. Then if further training succeeds in establishing a discrimination between the grey and the color, the inference is that this new discrimination is based on color vision. Breed (118, 119) used a method based on this principle with chicks, except that the original discrimination was a native and not an acquired one on the part of the chick. He employed light passed through colored screens, and offered the chicks a choice between two passages differently illuminated. They showed a preference which was evidently based on the relative brightness of the colors, since it could be reversed when the brightnesses were sufficiently altered. Then, when a blue and red were found between which the chick showed no preference, this was taken as an indication that they looked equally

bright to the chick. The bird could, however, be trained to choose one of these two colors; hence the conclusion was reached that while its first tendency was to react to brightness differences, it had the ability to distinguish color differences when training made such a proceeding worth its while. Reeves (853), experimenting on sunfish, used lights through colored filters, whose intensities were controlled by movable slits, and were measured. The first training of the fish was on different intensities of white light. When subsequently red and blue were used, a certain intensity of the red was found at which the percentage of correct choices fell to 50. This was taken to mean that the brightnesses were matched for the fish's eyes. Continued training with these two stimuli resulted in a rise of the percentage of correctness, indicating that the fish had the capacity for a red-blue color discrimination and could be taught to use it.

(e) The attempt may be made to train an animal to discriminate between a colored stimulus and a complete series of greys ranging from black to white; the greater the number of shades, the better. This is perhaps the most satisfactory method. It has been used in a number of investigations. Von Frisch (325), performing his experiments in the open air, trained bees to come to strips of yellow paper on which food was placed: he then mingled yellow strips, without food, among strips of thirty different shades of grey. The bees, he reported, were able to make the discrimination, and to do equally well when blue was used: they failed, however, with red, confusing bluish red with blue and dark red with dark grey. In another article (327), he says that a certain bluish red also was confused with grey, and infers that bees are red-green color-blind, having color-vision for blue and yellow. Hess (431) attacks these experiments by showing that the bluish-red paper used by von Frisch looks to a red color-blind human being quite unlike the blue paper used, the former appearing almost colorless and the latter much more saturated. Incidentally, he finds that if a checker-board pat-

tern of blue and yellow squares is used and the bees are accustomed to find food on the yellow squares, they do not, when no food is present, show any more interest in the yellow than in the blue. As we have seen, Hess ascribes the apparent ability of bees to see blue entirely to their sensitiveness to ultra-violet rays. This is an easy assertion to test, for it is easy to use screens, such as certain kinds of glass, which are impervious to ultra-violet rays. This was done both by von Frisch (331) and by Kühn and Pohl (56), and was found to have no effect on color-recognition. The last-named experimenters worked with spectral colors and varying intensities of white light: they trained bees to find food in a certain spectral color thrown on a table, and report that the bees could identify this spectral region when no food was present and when its location on the table was changed. They report no green-blindness: the bees could identify bluish-green and distinguish it from colorless light; Kühn (565) ascribes to them vision of four color-qualities, one produced by orange, yellow or green; one by bluish-green, one by bluish-violet and one by ultra-violet. House-flies also are red-blind and can be easily caught with the fingers in a room lighted with red; thus, at least, reports Wasmann (1044). Knoll (544) has used spectral light and white light in training a hawk-moth, and finds discrimination of blue and yellow, green being doubtful; he gets similar results from the butterfly Deilephila (545).

Burkamp (135) trained fish to take food from a tray of a certain color or grey, and tested them by placing a tray of the same color among twenty-four trays of different colors or greys, no food being present. The colors included various degrees of saturation, and whole series were made with different greys. He reports that the color-vision of the fish is like that of a human being.

Katz and Revesz (532) tested color vision in fowls by scattering grains stained red, blue, or green, in various saturations, mingled with grains stained four different shades of

grey. All the grains were stuck fast to the ground except those of a particular color, which the fowls thus had to learn to distinguish from the other colors and the greys. Their discriminative ability appeared about equal to that of a normal human being. The experiment is defective in that the number of grey shades was so small. Washburn and Abbott (1034) showed that rabbits could be taught, by being rewarded with food, to push a door on which a standard red paper was shown, rather than one which carried grey paper; but that they invariably failed when a very dark grey, almost black, was used. Only three shades of grey were employed; but obviously if one happens early in the proceedings to find a grey that can *not* be distinguished from a color, one's point is proved and further investigation with that color is unnecessary. Kittredge (541), using the same method, found that a bull-calf could not distinguish between red and very dark grey, a result which contravenes the established conviction that red irritates bulls.

Smith (935) argues in favor of color vision in the dog from the fact that the animals showed some evidence of learning to distinguish colors from all the greys used. De Voss and Ganson (249) report that none of the six colored papers they employed could be discriminated by cats from all the shades of grey in their series, each color being confused with some particular grey. De Haan (67) using colored papers and the multiple choice apparatus, finds that a Macacus monkey can distinguish red, green, blue, and yellow from all members of a series of thirty greys.

(f) The salivary reflex has been used by Pawlow and his pupils to investigate color-vision in the dog, no evidence for it being obtained (1123).

In addition to the precautions that must be used against the "brightness error" in experiments on color vision in animals, measures must also be taken, as in all tests of sensory discrimination, to guard against the use of smell, or of position in space, or of any other secondary clue to choice on

the animal's part. The use of colored papers has been criticised in cases where these were pasted on vessels for food or on compartment doors, because wrinkles might give clues; an obvious way of avoiding this is by pinning the papers on freshly each time. It has also been urged that differences in the surface texture may make differently colored papers reflect light in dissimilar ways. This possibility has been obviated sometimes by varnishing the papers (326), sometimes by introducing velvet in place of the paper in the midst of an experimental series (1035). It is evident that certain exact determinations can only be made with purely monochromatic light, such as no dyes or paints can give; on the other hand the use of spectral light, requiring darkness in the experiment room, makes the conditions more artificial and disquieting to the animal, and a good deal of valuable information about color vision can be obtained with colored papers.

§ 43. *Summary of Results for Different Animal Forms.*

It will be convenient to have a summary of the present state of our knowledge about the color sense of animals, considering each class of animals by itself. There is no satisfactory evidence of color vision in protozoa, cœlenterates, mollusks, or echinoderms. For annelids, we have only the doubtful evidence of the behavior of *Lineus ruber* in reversing chromatropism independently of phototropism. Difference of opinion among the authorities begins when we reach the crustacea; Hess arguing for total color-blindness, von Frisch, O. Koehler, and Minkiewicz for color vision. The latter authority (683) invokes as evidence the curious behavior of certain crabs (Maia), which have the instinct possessed by many crab species of attaching to their shells foreign objects, bits of seaweed and the like, which may serve the purpose of making them less conspicuous in their ordinary environment. When these crabs are kept for some time in

an aquarium lined with a certain color, their subsequent behavior is modified in two ways. (1) On being given bits of paper some of which are colored like the aquarium, while others are of a different color, the crabs select for decorative purposes the bits that match their surroundings. (2) When placed in another aquarium offering a choice between two compartments, one with walls matching those of the tank they have left, the other with differently colored walls, the crabs choose the former. Thus, at least, Minkiewicz found them to do. Two American investigators performed similar experiments. Pearse (779) failed to get any evidence that when crayfishes, spider crabs, crab spiders, and caddis fly larvæ are kept in colored boxes, they develop any tendency to choose later environment of the same color. On the other hand, Stevens (942), working with a Pacific coast crab which has the decorating instinct, finds that it does acquire such a tendency, but that it does *not* learn to decorate itself with colors matching its surroundings. That redoubtable antagonist of color-vision in invertebrates, Hess (433) also denies the occurrence of this latter behavior in crabs. In any case, such behavior would be no evidence of color vision, for the matching might be done by brightness.

No satisfying evidence of color vision in spiders exists: it has been shown that they prefer red when offered a choice of compartments illuminated through red, green, blue and yellow glass (782), and that they can form an association between colored paper and their nests (783), but no precautions were taken against the brightness error. On insects, we have Lubbock and Forel in the affirmative without eliminating sources of error, von Frisch and Knoll (544) holding the same opinion on better grounds, and Hess steadily in the negative. We have already noted the dispute as to how far visual sensations in general are involved in the reactions of bees to flowers, and have seen that Plateau maintains their relative unimportance in this connection, as compared to smell. Besides the experiments which we have quoted on p. 93, he

adduces the facts that he could never persuade insects to alight upon artificial flowers, though these were not distinguishable by human eyes from real ones (816-818); that bees show no preference for flowers of any particular color (819); and that they often make errors, in alighting on closed buds, seed pods, and wilted flowers, which indicate defective vision (821). But Josephine Wéry and others have noted that bees do seek artificial flowers (1060). Even Plateau does not deny that an insect may perceive flowers from a distance, whether because it sees the color in the same way that we do, or because it perceives some kind of contrast between the flowers and their surroundings (819).

Turning to the vertebrates, we find that the weight of evidence is decidedly in favor of color vision in fish; Hess alone maintaining color-blindness because of the distribution of physiological intensities in the spectrum. The fact that at the spawning season many fish assume bright colors and patterns has been discussed in this connection. Von Frisch (324) urges that such colors and patterns must have some influence in bringing the sexes together; Hess (423) points out that they would not be visible below a certain depth of water; von Frisch replies that most of the fish which display them spawn in shallower waters. A curious fear of red, or "red-shyness" was reported by Bauer (36), and Reeves (853) finds some evidence of special red avoidance, which may be due to its novelty (see p. 140). Von Frisch (335) has microscopically examined the retinas of fish immediately after they have made color discriminations: the results are highly important for the theory of color vision in general. In the light-adapted eye, he finds, the cones are pulled back into the plane of the image, while the rods are stretched out and partly buried in pigment: darkness adaptation reverses these conditions. His experiments showed that fish, like man, became color-blind in faint light, and his microscopical examinations showed that the transition from color-vision to color-blindness occurred just when the cones were thrust beyond the

image. Exceptions to this correspondence occurred with one species of fish examined.

Even Hess is willing to concede color-vision of the human type to the frog and the turtle. A special problem arises in connection with the study of color discrimination in turtles, birds, a few fishes, and the duck-billed platypus. In the retinas of these animals there are attached to the ends of the cones transparent colored globules like little drops of oil. They are in the turtle mostly red and orange, and are thought to act like spectacles of colored glass to cut off the blue and violet rays, so that turtles see the spectrum shortened at the violet end. Hess (418), in order to find out if this is the case, has tested turtles by illuminating their food with differently colored lights and observing under which lights they eat. He found that they did not eat in violet light, from which he infers that they could not see the food thus illuminated. We have here a method for determining the limits of visibility of the spectrum which will hold for animals that find their food exclusively by sight, and can be trusted not to eat in the dark.

Birds are unanimously agreed to have color vision, and the effect of the colored "oil globules" upon it has been much studied. The German observers are convinced that birds will not peck at food in the dark, and hence that the method of illuminating food with differently colored lights can be depended on to demonstrate the visibility of spectral colors: Breed (118) finds that chicks do peck in the dark. Hess (416) reports that the spectrum for day birds is shortened at the violet end, which would be the natural effect of their retinal globules; and that owls can see further towards the violet; the globules of night birds contain less red. Henning (403) has confirmed Hess's results for various birds and for turtles, and indulges in some ingenious speculations as to the usefulness of these curious globules. He points out that all animals can see red better than other colors through water and through mist; hence the reddened vision of the

concentrates red light rays
red rays & protection against ultra-violet rays

animals under consideration may be an adaptation to such conditions. He tested this by fastening colored masks on crows, owls, and pigeons, finding that those with red and yellow masks could find food better in a fog than those with blue and green masks. Erhard (282) has made the most careful study of the oil drops in the bird retina. To the fact that day birds have more orange drops and night birds many more bluish green ones, he adds that day birds of prey have fewer orange drops than do ordinary day birds. Tests with Hess's pupilloscope show corresponding differences in color discrimination: ordinary day birds are blue- and violet-blind, day birds of prey see more blue, night birds see little if any red. Erhard rejects Henning's theory of the usefulness of the globules in foggy weather, remarking that if it were true, red spectacles would be useful to the sailor! He holds that the globules help to secure the great keenness of vision which birds certainly possess, and which is due, he thinks, partly to the great number and fineness of their retinal cones, and partly to the action of the oil globules in collecting and concentrating the light, and in correcting by their color chromatic aberration. Incidentally, the blue-blindness of day birds shows that the blue color some of them possess can have no social significance. When it is looked at through orange spectacles, it of course becomes colorless, so the birds do not see each other as blue.

As for mammals, we should expect that color vision, which seems well distributed among the lower vertebrates and is so highly developed in man, would certainly be present; but the results, as we have seen, suggest color-blindness in every case investigated, except that of the monkeys.

§44. *Some Special Phenomena Connected with Visual Qualities.* *Darkness Adaptation.*

When the human eye has become "adapted" to darkness, two changes occur in vision: the eye becomes more sensitive to faint light; and, as we have seen, the brightest region of

the spectrum is shifted from yellow to yellow-green. Both of these changes apparently depend on an increased functioning of the rods of the retina as compared with the cones.

Hess (426) has found that the feet of starfish have their sensitiveness to light increased by being kept in darkness for some time. Daphnias which have been for a long time in the dark will respond to a lower intensity of light than those which have been long illuminated (236). Hess (433) notes the fact that the color-blind distribution of spectral brightnesses which he has found for Daphnia and its relatives holds for light-adapted animals. The dark-adapted eye of the frog shows a shift of spectral brightness like that in the dark-adapted normal human eye (449, 418). The observations of Katz and Revesz on the fowl (532) strengthen the evidence for its color-vision by showing that while fowls with light-adapted eyes pecked equally often at grains on yellow, green, red, and violet ground, those with dark-adapted eyes never pecked at grain on a red ground. Lashley (573), working with the Yerkes-Watson apparatus, also found that light-adapted chicks chose red and yellow rather than green, while for dark-adapted chicks the preference was reversed; all of which looks like the effect of darkness adaptation on a normal human eye. Honigmann (470) has made a careful study of the relation of darkness adaptation to the function of the oil globules in birds. The method was that of observing in what colors the birds would pick up grain. Light-adapted young fowls, he reported, see red as much lighter than do light-adapted human beings; that is, they picked up grains in red light so faint that human beings could not see. (This observation may be compared with Breed's (118) contention that fowls will pick up grains that they themselves cannot see). Soon after maturity, sensibility to the violet and blue lessens, probably on account of stronger absorption by the red globules. Under dark adaptation, the sensibility to light of all colors increased uniformly for the first fifteen minutes; after that the sensibility for the short

waves increased much more rapidly than that to other wavelengths. This means that after fifteen minutes the rods, which are more sensitive to violet and blue, and thus are held responsible for the shifting of brightness towards the blue end in the faint light spectrum for the normal eye and the daylight spectrum for the totally color-blind eye, come into increased function as compared with the cones, to which the oil globules are attached. This delay of fifteen minutes does not occur in the human eye. When man and the fowl are both fully dark-adapted, red, which looked brighter to the fowl than to man in the light, looks darker to the fowl. Erhard (282) confirms these results. That darkness adaptation is not always a function of the rods is indicated by the fact that it occurs in the turtle, whose retina has no rods (418).

Adaptation to colored light was observed in Burkamp's experiments on fish, described on page 155. After the fish have been trained to take food from trays of a certain color, if this color is used to illuminate the entire field, white trays should be sometimes chosen; that they were never chosen indicates, it is argued, a loss of sensitiveness to the illuminating light. Similarly, when the illumination was in a color complementary to the training color, it should have rendered trays of the training color hard to identify, but did not. Burkamp points out that adaptation to color would be very useful to creatures passing from one depth of water to another, where the absorption of light rays is different.

Negative after-images for both color and brightness stimuli are maintained by Ewald (290) to exist in Daphnia; the animals would reverse their reaction to the same white light according as they had been exposed previously to white (or blue) light, or to darkness (or yellow) light. Reichner (855) thinks he has shown colored negative after-images in fowls. The birds had been trained to eat in light of one color, and not to eat in the complementary color, the grains being glued to the ground in the latter case. After two minutes of eating

in the "eating" color, its saturation was suddenly greatly diminished: the fowls stopped pecking. Why? Because, Reichner argues, they saw a negative after-image of the "*verboten*" color!

Simultaneous brightness contrast is claimed by Ewald (290) in the case of Daphnia, from the observation that when the region surrounding a constant stimulus light is brightened, the animals make to the stimulus the reaction appropriate to darkening, and *vice versa*. The same phenomenon is interestingly shown in a hawk-moth (547). When night approaches, these insects seek the darkest place they can find, and sleep. Knoll found that they would alight on a dark disk on a white ground rather than on a similar disk on a ~~white~~ ground, and that they sought the edges of a large black disk on a white ground, presumably as the darkest region.

Simultaneous color contrast, according to Revesz (857) has been demonstrated in fowls: a fowl trained to pick corn off a green ground will pick it from the region surrounding a red ground.

The identity of the effect of intermittent and continuous lights of equal intensity, known as the Talbot-Plateau Law, is claimed by Ewald (288) to hold for the eyes of Daphnia; the animal's eye-movements were affected equally by interrupted and by continuous light. It is this law which enables us to measure the grey produced by a rapidly revolving disk of black and white sectors as equal in brightness to the amount of light reflected by the sectors at rest. The rate of rotation at which alternating black and white sectors must follow each other in order to fuse into a continuous grey was investigated by ~~Mast~~ in connection with the skin color changes in the flounder, and found to be the same for the fish's eye and the human eye. He placed the flounder over a rotating black and white disk and noted the speed of rotation required for the fish to become grey instead of mottled black and white (655).

We have seen that the ability of various animals to discriminate greys has been investigated in connection with the problem of color vision. Some experiments have been directed on this brightness discrimination for its own sake, as for instance by Reeves (853) on certain small fish; the general result is merely that the acuteness of such discrimination varies in different species. In his work on the dancing mouse, Yerkes (1113) established Weber's Law for brightness discriminations in the case of the one mouse he tested: the animal could distinguish a difference in the brightness of two compartments amounting to about one-tenth of their absolute brightness, within certain limits of absolute brightness. Erhard (281) finds that Weber's Law holds for the sensitiveness of certain lower crustacea to intensity differences, as shown in the degree of their positive reaction.

End

Mon. Jan. 30 - 1928

CHAPTER VIII
SPATIALLY DETERMINED REACTIONS

§ 45. *Classes of Spatially Determined Reactions*

MODIFICATION of the behavior of animals with reference to the spatial characteristics of the forces acting upon them appears at the very beginning of the scale of animal life, and throughout is quite as important as modification with reference to the kind or quality of such forces. It assumes a number of distinct forms. Some of these suggest to us, interpreting them as we must on the basis of our own experience, no conscious aspect at all; they seem rather mechanical effects upon a passive organism. In other cases, it appears possible that the mental process which we know as space perception, involving the simultaneous awareness of a number of sensations consciously referred to different points in space, may accompany the reaction of an animal with reference to the spatial relations of its environment. And sometimes we can only say that differences in the space characteristics of a stimulus may modify the accompanying sensation in some manner which yet apparently does not involve space perception as we know it.

Our task in the following pages will then be to examine the different ways in which animal behavior is adapted to the spatial characteristics of stimuli, and to ask which of these suggest as their conscious accompaniment some form of space perception. A classification of spatially determined responses that is not, indeed, ideally satisfactory, but may serve our purpose, divides them into five groups:—

1. Reactions adapted to the position of a single stimulus acting at a definite point on the body.

2. Reactions to a continuous stimulus, which involve the assumption of a certain position of the whole body with reference to the stimulus: orienting reactions.

3. Reactions to a stimulus that moves, i.e., that affects several neighboring points on the body successively.

4. Reactions adapted to the relative position of several stimuli acting simultaneously.

5. Reactions adapted to the distance of an object from the body.

These forms of behavior will be successively discussed.

§ 46. Class I: Reactions to a Single Localized Stimulus

Responses to stimulation that are adapted to the point of application of the stimulus are to be found among very simple animals. They may be subdivided into three groups: first, cases where the part of the animal that reacts is the part directly affected by the stimulus; second, cases where the whole animal reacts by a movement in the appropriate direction; and third, cases where a part of the body not directly affected by the stimulus moves toward the point stimulated.

1. Amœba furnishes an example of the first class. Its negative reaction occurs by the checking of protoplasmic flow at the point where a strong mechanical stimulus affects the body; its positive reaction by a flowing forward of the protoplasm at the point where a weak stimulus acts, and its food-taking reaction by an enveloping flow on both sides of the point stimulated. This would seem to be the most primitive way of adapting response to the location of a stimulus: the effect is produced just where the force acts, as it might be upon a piece of inanimate matter. In no animal with a nervous system, probably, is the process quite so simple. The bell of the jelly-fish contracts at the point where a stimulus, mechanical or photic, is applied; yet although these responses are made when the nervous system is thrown out of function, they occur more slowly, and in the normal animal the nervous tissue is prob-

ably involved, while, of course, a long conduction pathway is traversed when, to use a familiar illustration, the baby pulls back its hand from the candle flame.

2. Paramecium and other infusoria, planarians, the earthworm, and various other animals give us illustrations of movements of the entire body differing according to the point affected by a single stimulus. If the front half of Paramecium be touched, the animal gives the typical avoiding reaction of darting backward and turning to one side; if the hinder end be touched, it moves forward (512, p. 59). On the other hand, it makes no difference in its reactions to stimuli affecting either side of the body; the turning is always to the aboral side even when the stimulus comes from that direction (512, p. 52). If strong mechanical stimulation be applied to the head end of a planarian, there is a response which seems to belong under type (1): the head is turned away from the stimulus. If the hinder region is touched, strong forward crawling movements of the body are produced. The positive reaction in the planarian, turning the head toward the stimulus, also suggests type (1), but in reality it has been shown by Pearl to be a far more complex affair than the mere flow of protoplasm at the stimulated point, and to involve the contraction of several sets of muscles (773). The earthworm creeps backward if the front half of the body is affected, turns away from a stimulus applied to the side of the anterior end, and creeps forward if the stimulus affects the posterior half of the body (511). In general, a reaction of type (2) rather than type (1) will occur in proportion to the degree in which an organism's movements are coördinated and it tends to act as a whole.

3. One of the prettiest examples of the most highly co-ordinated form of response to a single localized stimulus; namely, movement of some other part of the body toward the point affected, is to be found in the swinging over of the jellyfish's manubrium toward the spot on the bell touched by food. "In the typical feeding reaction," says Yerkes, "the

manubrium bends toward the food. If during such a movement the piece of food be moved to the opposite side of the bell, the manubrium, too, in a few seconds will bend in the opposite direction, that is, again toward the food" (1095). The sea urchin responds to mechanical stimulation by moving the spines toward the place stimulated (1000). In the higher animals this form of reaction has largely superseded other methods of adapting behavior to a stimulus acting at a definite point. Where grasping appendages exist, the obvious device is to move them toward the point of stimulation in order either to seize or to remove the object. This involves not merely that the effects of the stimulus shall diffuse so as to involve general locomotor movements, but that the effect shall be exerted very definitely upon a particular set of muscles in a particular way. The "scratch-reflex" of mammals, and the reaction whereby a frog rubs its hind leg on the spot of skin affected by a drop of acid, are further examples.

What can we say regarding the conscious accompaniment of the reactions described under these three heads? When a stimulus applied at point *a* brings about a reaction different from that produced by precisely the same stimulus acting on point *b*, are the accompanying sensations different, supposing the animal concerned to be conscious? If they are, the difference must be what has been called a difference in local sign. There is certainly no evidence that space perception is concerned. Space perception in our own experience always involves the simultaneous awareness of several stimuli. But where a single stimulus only is operative, the fact that reaction to it is modified by its location cannot mean that the relations of that location to the location of other stimuli are perceived. The truth is that space perception is so constant a factor in our own experience that we cannot imagine how a single sensation can be modified in connection with change of place of the stimulus, where space perception does not exist. A touch at any point on the skin of a human being is referred

to a definite point in a spatial pattern, tactile and visual; it is given its proper place in a complex of sensations. What modification of it would correspond to its location if it stood alone in consciousness, we cannot now conceive.

§. 47. Class II: Orienting Reactions; Possible Modes of Producing Them

Various forces, such as gravity, light, electricity, centrifugal force, currents of water and air, are all influences causing certain organisms to bring their bodies into a definite position. Such reactions, involving the direction of the whole body with reference to a continuous force acting upon it, are known as reactions of orientation. There are various ways in which they might conceivably take place.

(a) They might be due to the "pull" of a force upon the passive body of an animal. In the case of gravity or of a current of wind or water, if one part of the body were heavier or offered more surface to the force, the position assumed could be explained without supposing any activity on the animal's part. In such a case there would be no reason for thinking of the reaction as conscious.

(b) The response might be due to the effect of a force acting unevenly upon the two sides of the body, and thereby unevenly affecting the motor apparatus on the two sides, thus causing the animal to turn until the forces acting upon symmetrical points were balanced. This, although involving activity on the animal's part, would not, if the force acted directly on the muscles, suggest any conscious accompaniment. If it acted through symmetrically placed sense organs, awareness of the direction from which the force operated might be present.

(c) The orientation might take place by a negative reaction on the animal's part to a definite stimulus given when the animal was in any other than the final, oriented position. If gravity were the force in question, the stimulus might be the pressure exerted within the body by particles of different

density or by the fluid or mineral bodies in a statocyst organ. If the stimulus were light, the organism might be oriented by giving the negative reaction when its head entered a region either brighter or darker than the optimum illumination. In such cases, where the ordinary negative reaction is the only one involved, there is no reason to suppose the occurrence of any conscious accompaniment, other than the possible unpleasantness connected with that reaction.

(d) Orientation to gravity might occur through a specialized "righting" reaction, given in response either to a stimulus within, say, a statolith organ, or, as in the planarian, to the absence of accustomed contact stimulation on one surface of the body. The reaction in these cases being a specialized one, it is possible that a peculiar sensation quality might be involved.

(e) Orientation might take place through a movement occurring when the position of several stimuli perceived simultaneously was disturbed, and tending to restore them to their original position. This is the principle involved, as we shall see, in explaining the rheotropism or current orientation of fishes, and the anemotropism, or orientation to air currents, of insects, as due to an instinct to keep the visual surroundings the same. And this form of orientation alone suggests a true space perception as its conscious accompaniment.

Such being the conceivable ways in which orientation may be brought about, what are the observed facts? They may be considered under the heads of orientation to gravity, to light, and to other forces.

§ 48. Orientation to Gravity: Protozoa

To this form of reaction the term "geotropism" or "geotaxis" has been applied. In various Protozoa negative geotropism, or a tendency to rise against the pull of gravity, has been observed: first by Schwartz in two single-celled organisms frequently classified as plants, Euglena and Chlamydo-

monas (912); and eight years later by Aderhold, who suggested, without accepting it, the theory that the orientation may be due simply to the greater weight of one end of the organism's body (3). This view was maintained by Verworn: the action of gravity, he urged, must be purely passive. It cannot operate as a stimulus to active response on the animal's part, for a stimulus is always a change in environment, and gravity is a constant force (1011). This ignores the fact that the animal's relations to gravity may change though gravity does not, and also the fact that the continuous action of light is a stimulus. According to Verworn's theory, the geotropic orientation of a single-celled organism takes place through a series of "little falls" whereby the heavier end is directed downward. Massart opposed this view on the basis of observations which showed that the actual movements of the organisms did not correspond to it, but were the result of active orientation. If response to gravity is passive, then dead animals should fall through the water in the same position as that assumed by living animals when oriented to gravity. Massart experimented with various Protozoa by killing them and studying their positions in sinking, which he found not always the same as the attitudes assumed in response to gravity (641). There is always the possibility, however, that the methods employed to kill may change the specific gravity of some part of the body. Jensen offered the theory that reaction to gravity may be due to the difference in the water pressure on the two ends of the animal. He asserted that when the air pressure on the water was reduced by exhausting the air above, there was an increase in the geotropism, indicating a relative rather than an absolute sensibility to pressure (515), but Lyon points out that this process may affect the animals in various other ways besides altering the air pressure. Increasing the air pressure, or protecting the surface with oil, has no effect upon geotropism, Lyon finds, and he urges that Jensen's theory requires enormous sensibility to pressure differences on the organism's part, as great as that

several aspects of orientation are due to the body's unequal sensitivity to pressure. Continuous stimulus is due upon symmetrical part of the body, but to each side of the organism by trial and error. Intermittent stimuli and adjustment of the organism by trial and error to each successive stimulus.

needed by a human being to note the difference between the air pressure on the head and that on the feet (617). Another suggestion was offered by Davenport (237), namely, that negatively geotropic organisms swim in the direction where the greatest resistance to their progress is offered. This is like one theory put forward to explain rheotropism, or the tendency of animals to swim against currents, and anemotropism, or the "head against wind" movement of insects; and as Rádl (842) first and Lyon (616) afterward pointed out, it assumes the fact to be explained, for only if an animal actively opposes a force, will that force exert more pressure at one point of its body than at another. The theory cannot explain why an animal at rest should be oriented. Another argument that tells against it is offered by experiments showing that animals placed in solutions of the same density as their own bodies, in which, therefore, they have no weight, still display negative geotropism, and that the direction of the response is not reversed when the fluid is made heavier than the animals (617). Lyon's own theory, accepted by Jennings, is that the stimulus for geotropism is furnished by the action of gravity within the body of the organism, upon substances of different weight which exert varying pressures and take up different positions according to the position of the body (617).

Harper (392) in 1911 revived the mechanical theory of the geotropism of Paramecium. He urged that an animal which, like this protozoön, moved in a spiral could hardly use the changes of position of internal particles as effective stimuli. The reaction of Paramecium can be altered by altering the specific gravity of its body, as by causing it to absorb particles of iron or paraffin. When it has ingested iron, its responses are modified by the neighborhood of a magnet (393). Wager (1023) maintains that geotropism in Euglena also is purely passive, due to the fact that the hinder end of the animal is the heavier. Kanda (525) has recently championed the "statocyst" theory of Lyon, as against the mechanical theory, using Lyon's argument that when Paramecia are rapidly ro-

tated in an apparatus called a "centrifuge," their front ends are directed outward by centrifugal force and therefore must be heavier, instead of lighter, as the mechanical theory would require. Harper had previously attempted to meet this objection by regarding such a position on the part of the centrifuged animals as due not to centrifugal force but to compensatory movements made actively by the animal. Both the mechanical theory and the "statocyst" theory, then, seem to be still on the field.

It has been shown that the reactions of Paramecium to gravity are modified by a variety of conditions. Negative geotropism, in a sense its normal condition, is favored by plentiful food supply and by an increase in temperature within certain limits; positive geotropism, movement downward, may be brought about temporarily by mechanical shock, by salts and alkalies, by temperature changes (697, 937), to which, however, the animals may adapt themselves; with less constancy by increase in the density of the fluid containing them, and with lasting effect by lack of food. It has been suggested that the downward movement under these circumstances is protective, since it shields the animals from surface agitation of the water, from surface ice, and from failure of the surface food supply (694). We shall see that similar conditions often change the direction of an animal's response to light.

Schaefer (894) denies that positive geotropism exists in Paramecium: what really occurs is the failure of negative geotropism.

§ 49. *Orientation to Gravity: Cœlenterates*

Among the cœlenterates, geotropism is shown by certain hydroids, whose stems have a tendency to curve upward and their "roots" a tendency to grow vertically downward when the animals are placed in a horizontal position (975). The sea-anemone *Cerianthus*, whose normal position is head up-

ward, will right itself if placed in any other position, though the righting reaction may be inhibited by contact stimulation on the side of the animal. It ordinarily lives with the body enclosed in a tube, and when taken from its proper habitat it seems to "prefer" a position, even horizontal, where the sides of the body are in contact with a solid, to a vertical position with its sides uncovered (590). The righting reaction of Hydra is not determined by gravity at all; the animal will take any position, vertical or horizontal, but "seeks" always to have its foot in contact with a solid (1024). Some actinians have shown an interesting modification of gravity reaction through what we may call habit. Six specimens of *Actinia equina* were selected that had been fixed to the rocks in an "upside-down" position, that is, with the mouth end downward; and six others that had been right side up. In the first experiment all were placed upside down; the tendency to right themselves was decidedly stronger in those which had been previously erect. Similarly, when twelve selected in the same way were all placed right side up, the ones that had previously been in the reversed position showed a certain inclination to reassume it (350). On the other hand, the orientation of the polyp *Corymorpha palma* to gravity was entirely unaffected by keeping the animal for a long time in a position where it could not right itself; it assumed the upright position as soon as it was set free (975).

It was noted in the chapter on hearing that the peculiar organs occurring in certain Coelenterata and in many other animals, which were originally called otocysts because of their supposed auditory function, have had their name changed to that of statocyst since it has appeared that they subserve chiefly orientation to gravity. In jellyfish, Murbach and Nagel report that removal of these organs does not affect the animal's power of keeping its balance; apparently equilibrium is maintained here by the simple action of gravity, for dead jellyfish float in the right-side up position (714, 721). Frankel (313), on the other hand, says that the upright position is held

by compensating movements, the striking of the statoliths against their sheaths being the stimulus. It has been suggested that the statocyst organs are for the reception of stimuli produced by shaking, to which medusæ are apparently sensitive (721). Negative geotropism exists in *Gonionemus*, which swims to the surface of the water when disturbed (1118). In ctenophors, the statocyst organ, which is usually at one pole of the body, has been found to function as an organ for the maintenance of equilibrium (1010).

§ 50. *Orientation to Gravity: Planarians*

A good example of a specially developed reaction having for its result the "righting" of an animal in an abnormal position is offered by the behavior of a planarian that has been turned over so that its back rests on the surface of support. The reaction consists of a turning of the body, beginning with the head end, about the long axis, so that a spiral form is assumed. The dorsal surface of the animal is convex, the greatest thickness of the body being in the middle line. When the planarian lies on its back, it thus naturally tips to one side, like a keeled boat out of water. This side, being brought into contact with a solid, gives a reaction analogous to the negative one, that is, it extends or stretches. Such a stretching of one side when the planarian is right side up would of course produce a turning in the opposite direction, a negative reaction. In this case, however, the opposite side does not contract to allow of turning, but maintains the same length. The necessary result is that the body is thrown into a spiral: as soon as the ventral surface of the head comes into contact with the solid, in consequence of the turning, the negative reaction of that end ceases. Thus the righting is progressively accomplished (773). The whole response can hardly be classed under the head of geotropism. Like that of *Hydra*, it is not made as the result of the pull of gravity, but is a reaction to contact stimulation; the animal will crawl in an upside-down posi-

tion as readily as any other provided that the ventral surface and not the dorsal is in contact with a support.

Olmsted (732) finds true geotropism in the planarian, determined by its fed or unfed condition and by previous exposure to light.

§ 51. *Orientation to Gravity: Annelids*

Geotropism, in the marine worm *Convoluta roscoffensis*, has been found to fluctuate with the rise and fall of the tides, even when the animal is removed to an aquarium. In normal life the worms burrow in the sands at rising water, and come to the surface when the tide retreats. Prolonged exposure to air, or increase in the intensity of the light, causes them to move down the slope of the shore to moist places. These movements in the normal environment are represented by upward and downward movements of the animal when confined in a glass tube. Keeble and Gamble thought these oscillations in geotropism did not occur in darkness, and that the stimulus bringing them about was photic. When the summation of light stimuli passes a certain amount, they maintained, positive geotropism appears; when the after effect of light stimulation is dissipated, the negative phase recurs (342). Bohn, however, finds that the oscillations do persist in darkness, and that their primary cause is the mechanical shock of the waves, as is further indicated by the observation that shaking the tube will cause the worms to descend (77). The geotropism of *Convoluta* is dependent on the statocyst (342).

§ 52. *Orientation to Gravity: Mollusks*

Among Mollusks, the slug has had its reactions to gravity carefully observed. When placed in a horizontal position on an inclined glass plate, these animals tend to turn either upward or downward, moving either with or against the force of gravity. Davenport and Perkins found that the same individuals differed at different times in this respect, and con-

cluded that the sense of the geotropism was determined by obscure conditions. They also found that an inclination of only 7.5° on the part of the glass plate, representing only 13° of the full force of gravity, is sufficient to make the slugs orient themselves with reference to the pull of the earth, though the precision of such orientation increases as the angle increases (237). Frandsen thought it was the weight of the posterior part of the body that determined whether the movement should be up or down: that the natural tendency of all was to go downward, but that in some individuals the posterior part, which is poorly controlled, was heavier than the anterior, and pulled the animal around head upward (317).

Kanda (528, 529), on the other hand, thinks that in freshwater and marine snails the statoliths are the organs determining orientation to gravity, and that it is not merely passive: he claims to have observed that this orientation is most marked, the less the slope of the surface on which the animal crawls. The response of *Physa*, a freshwater snail, to gravity depends in an interesting way on the animal's physiological condition: when the snail is in need of air it is strongly negative in its geotropism, crawling upward towards the surface of the water and disregarding all other stimuli: as soon as its lungs are full of air it is no longer sensitive to gravity (239).

Cole (189) has neatly demonstrated that the essential stimulus in the snail *Helix* for geotropic orientation and movement is the tension of the body muscles produced by the downward pull of gravity, rather than the statolith apparatus. He showed that the rate of orientation and movement upward was increased by loading the shell, a condition that would increase muscular tension but could have no effect on statoliths. Budenbrock (127, 128, 129) and Baunacke (38-40) have brought evidence to support the view that the statocysts in many mollusks are useful not so much in securing orientation to gravity, which is of little importance in such slow-moving animals, but rather in enabling them to right themselves, to direct their movements, and to dig in the sand. The statocyst organs in

a cephalopod, *Eledone*, have been shown to function in maintaining equilibrium (337).

§ 53. *Orientation to Gravity: Echinoderms*

Righting reactions in the starfish have been described by Romanes (873). The tips of two or three rays are twisted around until the suckers in the ventral side have a firm hold of the supporting surface; the twisting is then continued, always in the same direction on the different rays, until the whole body is turned. Jennings (514) enumerates twelve different factors which determine which particular rays shall twist over and attach themselves first, but Moore (694) thinks that the "positive stereotropism," that is, the tendency to remain in contact with solids, of the tube feet is a sufficient explanation. It is not clear how a tendency to *remain* in contact with a mechanical stimulus can explain a tendency to *seek* such a stimulus when it is absent, and Jennings's view, that the original impulse to turn comes from the general state of unrest in which the animal is thrown by its position, seems plausible. But what is the stimulus inducing the unrest? Not contact of the back with a solid object, for a starfish is not disturbed if its back is touched when it is crawling in the ordinary position; and not merely having its back directed downward, for it will crawl upside down on the under surface of rocks. Something abnormal about the stimulation of the tube feet when they are in contact, not with a solid support, but with the water flowing over them, must present the condition for the internal state of instability which occasions the twisting movements of the rays.

The sea-urchin, "a rigid, non-muscular, and globular mass," as Romanes calls it, with relatively feeble suckers, has a much harder time to right itself, and does not succeed in pulling itself over unless it is perfectly fresh and vigorous. It occasionally rests for some time when it has reached a position of stability halfway over, before continuing the process (873).

Parker (759) thinks the spines function as statocysts in *Centrechinus*.

Lyon has observed marked negative geotropism in the larvæ of the sea urchin. He was unable to test Davenport's theory of the nature of the geotropic response by putting the animals in a solution of the same density as their own bodies, for the reason that such a fluid was too dense and sticky (being made of gum arabic and sea water) for them to swim in. That the response was merely a passive one he thinks improbable, because the larvæ from eggs that have been rapidly rotated, or "centrifuged," as it is called, have all the pigment on one side of their bodies and may therefore be supposed to have their ordinary balance disturbed; yet they rise to the surface just like the rest (618).

E. M. M.

§ 54. *Orientation to Gravity: Crustacea*

That the statocyst organs in Crustacea are probably connected with equilibrium rather than with hearing we have already seen. Delage in 1887 found that *Mysis*, *Palæmon*, and other forms displayed serious disturbance of equilibrium when both eyes and statocysts were destroyed, showing that the eyes also play a part in the maintaining of balance (244). The eyes have been found to coöperate with the statocysts in the fiddler crab, *Gelasimus*, and also in another decapod, *Platyonichus* (173). Neither of these has statoliths. *Penæus membranæus*, on the other hand, was found to be permanently disoriented by destruction of the statocysts or even removal of the statoliths, while blinding produced no great disturbance, probably because of the animal's nocturnal habits (47, 338). Young crayfish with the statocysts destroyed will swim upside down as readily as right side up (134). But the prettiest evidence for the static function of the statocysts was obtained when powdered iron was substituted for the mineral bodies in the open statocysts of *Palæmon*. It was found that when a magnet was brought near, the animal would respond by taking

up a position corresponding to the resultant of the pull of the magnet and that of gravity (559).

Specific righting reactions occur in many Crustacea, though in some cases these seem to be merely the incidental effects of ordinary locomotion. Branchipus, the fairy shrimp, normally swims upside down; if turned right side up when moving along the bottom of the vessel, it continues to move in this position without showing any disturbance until it happens to rise a little from the bottom, when apparently the weight of the body pulls it around into the usual upside-down position. The crayfish has two methods of righting itself: a quick "flop" executed with the tail, and a slow and laborious raising of itself on one side and tipping over (241).

Many Crustacea show marked responses to gravity: for example, Parker found decided negative geotropism in the females of the marine copepods whose depth migrations he studied. It seems to be needed to counteract the tendency of the animals to fall to the bottom by their own weight (740). In certain copepods, light was observed to change the sense of the response to gravity, not by taking its place as a directive stimulus, but apparently by producing some physiological change in the animals. Their normal geotropism was positive, that is, they had a tendency to move downwards. In darkness, however, their geotropism became negative. They were also negatively phototropic to strong light. If, when in the negatively geotropic phase, they were illuminated from below by intense light, from which they would ordinarily have moved away, the change from negative to positive geotropism induced by the light was of sufficient influence to make them move downward toward it (286). Other facts regarding the relation of geotropism and phototropism are mentioned on pp. 204 f.

§ 55. *Orientation to Gravity: Spiders and Insects*

Spiders and insects have no statolith organs. Bethé thinks that equilibrium is maintained in their case as a natural re-

sult of the position of the centre of gravity and the distribution of air in the body. He supports this view by experiments in which dead insects, allowed to fall through the air, assume the normal position, and is inclined to think that all animals without special static organs maintain their balance in this way (58). Negative geotropism in certain insects, as evinced by a tendency to creep from horizontal planes up vertical ones, was observed by Loeb (586). Cole (186) finds that the fruit-fly, when creeping, reacts negatively to gravity, and thinks that the stimulus is received by the leg muscles. In light the eyes of insects have probably much to do with maintaining equilibrium. Certain aquatic insects, in experiments where the light was made to strike them only from below, as soon as they left the support on which they were resting turned themselves upside down (842).

It has been held that caterpillars which feed on the leaves of plants, but hatch on the ground, find their food by negative geotropism which leads them to climb trees, but Hess (434) maintains that there is no such thing as a negatively geotropic caterpillar; their responses are determined by light.

§ 56. *Orientation to Gravity: Vertebrates*

It has long been known that in vertebrates the static function resides in the ear, and especially in the semicircular canals (*e.g.*, 120, 223, 305, 358). Various experimenters have noted that operations on the ears of fishes disturb the equilibrium of these animals. Sewall, indeed, found that section of the semicircular canals in the shark had no effect on its balancing powers, although operations on the vestibule and ampullæ did disturb movement (915); and Steiner got no effect on equilibrium from removing the contents of the labyrinth (941). Errors in methods and observation probably influenced these results. Loeb found that severing the auditory nerve or removing the statolith from the dogfish caused the fish to incline toward the operated side and to roll the eyes in that direction

(590). Total extirpation of one labyrinth in the perch was observed by Bethe to make the fish curve toward the affected side. The fish *Scardinius* showed a tendency to curve toward the opposite side (58). Lee's experiments on the dogfish showed a very definite relation between the position of the canal operated upon and rolling movements of the fish. Cutting the front canals caused the fish to dive forward, cutting the rear canals made it dive backward, and cutting the canal on either side made it roll over toward that side. A natural explanation of this behavior is to suppose that the absence of stimulus from the cut canal produces the same effect that rolling the fish in the opposite direction, and thus diminishing the pressure of the fluid in the canal, would produce. The fish "feels as if" it were being rolled over, and makes movements to regain its equilibrium. When the nerves supplying the ears on both sides were cut, the fish became perfectly indifferent to its position and would float upside down without any effort to right itself. The vestibule and otoliths of the fish ear are thought by Lee to be concerned with static equilibrium; that is, with the maintenance of position while the fish is at rest, while the canals are concerned with balance during motion (dynamic equilibrium) (580). It may be added that experiments on the sea horse indicate that destruction of the labyrinths in this animal has no effect on equilibrium: the upright attitude is due to the position of the air bladder and is assumed even by dead animals (339).

That vision may materially aid in maintaining equilibrium in vertebrates is indicated by evidence from various sources, among others, the observation of Bigelow that goldfish in which the nerves supplying both ears had been cut recovered after two or three weeks and could swim quite normally except when they were placed in a large body of water and made to swim rapidly, when they showed no power of preserving their balance (68). Their successful performance of slower movements was very likely due to the use of sight.

Sensory impulses from the body muscles themselves un-

doubtedly coöperate with those from the semicircular canals in the maintenance of balance. They are evidently involved in the peculiar withdrawing movements by which land animals, even puppies, kittens, and young rats whose eyes have not opened, save themselves from falling when they reach the edge of the object on which they have been crawling (680, 931). Water-dwelling animals, accustomed to plunge off solid supports, lack this protective instinct; Yerkes showed that among several species of tortoises, some land-dwelling, some amphibious, and some aquatic, the first mentioned were much more reluctant than the second to crawl off the edge of a board, and the second more reluctant than the third (1103).

§ 57. *The Psychic Aspect of Orientation to Gravity*

Glancing back over these examples of the responses made by animals to gravity, we note that while in some cases the earth's attraction appears to act mechanically upon the animal, causing the body passively to assume a certain position, the common method of bringing about orientation seems to be that some structure in the body, placed in an abnormal position, presents a stimulus which brings about a compensatory movement. This structure may be heavier particles of the body substance, as probably is the case in *Paramecium*; it may be a statolith, or the fluid in the labyrinth; it may be the eyes. In any case, what shall we say about the sensation quality involved? Perhaps the reactions produced are wholly reflex. Perhaps the statolith or the canal fluid produces a specific sensation quality. Or perhaps, as Verworn thinks, the sensation quality is merely that of pressure (1010). Whatever its nature, spatial perception, the perception of the spatial relations between several stimuli simultaneously apprehended, plays no part in the orientation of animals to gravity.

§ 58. Orientation to Light

In some animals light is sought or avoided not simply because of the fact that in certain intensities it stimulates to restlessness and activity (photokinesis), so that they come to rest in regions illuminated by other intensities; but through a direct movement of the animal towards or away from the source of light. It is this type of response to which Loeb and his followers restrict the term "tropism." Plants show it, both in the orienting of their stems with relation to light, and in the movements of their freely swimming "swarm spores." In the case of animals, it is illustrated by the behavior of the sea-anemone *Actinia cereus*. Weak light causes expansion of the tentacles of this organism perpendicularly to the light rays. If the light is increased, Bohn (102) says the tentacles "tend to orient themselves in the direction of the rays, and finally converge in a bundle parallel to that direction," a response which has the effect of protecting them from the intense light. Again, the tube-dwelling worm *Spirographis spallanzanii* gradually curves its tube until its mouth end faces the direction from which the rays of light come, and another marine worm, whose tube is absolutely stiff, adapts itself to a change in the direction of the rays by curving the newly formed portions of the tube as it constructs them (588).¹ Sea-anemones and tube-dwelling worms closely resemble plants in their mode of living. In freely moving animals, where the oriented movement is made in response to light, it is commonly preceded by body orientation; that is, the body first faces or turns tail to the light, and the animal then moves forward. Sometimes, however, there is no regular body orientation; the animal moves, for instance, always away from the light, which means that it moves forward if its body happens to be oriented with the tail to the light, or backward if its head happens to be directed to the light. Such behavior is

¹Hargitt (391) finds no such constancy of orientation in *Spirographis* as would warrant Loeb's calling the motion a tropism.

reported by Holmes of mosquito larvæ (465) and by Gee of leeches (349). On the other hand, Hadley (372) says that young lobsters always orient with the head towards the light, though they may move either away from or towards it. In some animals with eyes, such as the crustacean *Daphnia*, there is reason to think that body orientation is primarily an affair of *eye-orientation* or fixation. This at least is the view of Rádl (841). He placed *Daphnia* under a microscope in such a way that only the eyes could be moved. When the light coming from below was diminished, the eyes rolled upward; when the light coming from above was diminished, the eyes rolled downward. Holmes (456) observed that in amphipods, blackening one eye of a positively phototropic animal causes a turning toward the blackened side, as if the animal were trying to restore the missing illumination; similar experiments upon negative animals produced turning towards the other side.

It is the view of Loeb (600) that oriented response of animals to light is wholly analogous to the same type of response in plants. Since plants with their very slow and limited movements are subject more to light as a continuous stimulus than to sudden changes in light intensity, orientation in their case must be brought about by the steady and continuous action of the light. Accordingly, Loeb maintains the view that *phototropism or oriented response of animals to light is dependent on the continuous action of the light, and not on changes in light intensity*. It is thus a mode of response that has nothing in common with "sensibility to difference," which Loeb recognizes as an independent form of reaction, but occurs by method (b), described on page 170, rather than by method (c).

In support of this continuous action theory Loeb lays great stress on the proof, by the botanist Blauuw, that the "Bunsen-Roscoe Law," that is, the law that the effect of weak light acting a long time is equal to that of strong light acting a short time, holds for plants; Loeb thinks it holds also for animals. On this point there is difference of opinion. For

example, the reactions of tadpoles (730) and of the sea-anemone *Cerianthus* (700) are found to obey the law, but Mast (661) says of the orientation to light in the drone-fly and robber-fly, "All reactions are in accord with the Bunsen-Roscoe law in certain respects, but none are in accord with it in all respects."

Loeb is also interested, in connection with proving the identity of the orienting effect of light on plants and on animals, to show that the distribution of physiological effectiveness in the spectrum is the same for plants and such animals as show tropisms. In plants, the most effective region is the blue: in human beings, as we have seen, it is the yellow, and in color-blind human beings, the yellow-green. The results of many investigations of this problem for various animal forms were discussed in Chapter VII. Mast (654), using two beams of light which fall on the animal at right angles to each other, and which differ in color while equal in intensity, found that some animal forms, such as the larvæ of the blow-fly, are most strongly stimulated by that region of the spectrum which acts most strongly on the color-blind human being, while others, such as the earthworm and the larvæ of the worm *Arenicola*, are like plants most responsive to blue. The possible relation of the ultra-violet rays to these facts will be recalled. Hess (429), as we have seen, thinks he has demonstrated in the case of many animals subject to phototropism the superior effectiveness of yellow-green light.

On the supposition that phototropism is, as Loeb holds, due to the continuous action of light, the influence of such light in producing a tropism has been explained in two ways: (1) as the effect of the *direction* of the light rays traversing the animal's body, and (2) as the effect of having symmetrical points on the animal's body stimulated with *unequal degrees of intensity*. In his earliest discussion of the subject, Loeb (585) expressed himself positively in favor of the former hypothesis. "The orientation of animals to a source of light is, like that of plants, conditioned by the direction in which the light rays

traverse the animal tissue, and not by the difference in the light intensity on the different sides of the animal." Bohn, in general the ardent follower of Loeb, urged as a "fundamental objection" to this that "the 'luminous rays' which strike a living body have, save in wholly exceptional cases, various directions, being reflected, diffused, and refracted by neighboring bodies" (96). Moreover, those animal bodies which are opaque could not be traversed by light rays. Loeb seems later to have abandoned the "direction theory" of the tropism. The "intensity theory" was first proposed by Verworn (1012).

How can differences in the intensity of a stimulus falling upon symmetrical and opposite points on an animal's body bring about orientation? Let us call the two points a and a' , a being a point on the right side of the animal's body and a' a symmetrically placed point on the left side. Suppose the animal has a tendency to orient itself positively to the light, that is, turn towards the light, and suppose a ray of light strikes it obliquely from the right. Evidently the point a receives a greater intensity of the stimulus than the point a' . Now if the animal is positive to light, Loeb would suppose that its chemical constitution is such that light causes, either by direct action on the muscles or reflexly through the eyes, a contraction of the muscles. Hence the muscles at point a , or controlled through point a , would contract more strongly than those at point a' : the animal in consequence would turn towards the right, that is, towards the light, and would continue so turning until the light struck a and a' with equal intensity, that is, until it directly faced the light. All subsequent movement would have to be directed straight towards the light. If the animal is negative in its response to light, then it is so chemically constituted that light causes a relaxation of the muscles. In such a case, the point least strongly stimulated would produce the strongest muscular contractions: the animal would turn towards that side, and would continue turning until opposite points were equally stimulated, that is, until it

headed directly away from the light: all subsequent movement would have to be in this direction.

Opposing the continuous action theory of Loeb, Jennings (507), has suggested that *the oriented reactions of certain organisms, at least, are really due to changes in the intensity of the light, brought about by the animal's own movements.* This view would, if generalized, put all directed light reactions in the "sensibility to difference" class, given to changes in intensity: the effect of continuous light would be limited to photokinesis. Jennings, in other words, accepts explanation (c), described on page 170.

Let us see how an oriented response may be conceived to result from reactions to changes in light intensity. In the Protozoa, according to Jennings (507) and Mast (643), the orientation is due to negative reactions given when the organism in its ordinary swimming movements, which usually involve turning from side to side, either passes into a region of greater or less illumination, or swings its anterior end "toward or away from the source of light, so that it is shaded at one moment and strongly illuminated at the next." Suppose, that is, an animal makes in its locomotion slight random movements of the head from side to side. Suppose that one side of it is more brightly illuminated than the other. If the animal is positive to light, it has the characteristic of making a negative response whenever its head end is suddenly darkened. This will happen when the head end is accidentally turned away from the light; consequently all such random movements will be checked, while random movements of the head towards the light will not be checked. Hence the animal will turn until its head points towards the light: in this position random movements towards either side will be equally checked because they will equally tend to bring the head into a darker region; and so movement will take place in a line generally towards the light, though still with balanced random movements to either side. If the animal is negative, it has the characteristic of making negative reactions when the illumination of the head

is suddenly increased, and obviously this will bring about orientation with the head end away from the light.

In *Volvox* (see page 126), orientation is held by Oltmanns (731) and Mast (644) to occur after this fashion. The reaction of a *Volvox* colony, which in moderate light is positively phototropic, takes place in consequence of a response by each individual in the colony given when, as the colony rotates, that individual passes from a higher to a lower intensity of light.

When the "direction theory" of the tropism was receiving more attention than at present, evidence that an animal oriented in response to the direction of the light rather than to the comparative intensity of stimulation on symmetrical points was taken as arguing against Jennings's view of the tropism as a response to changes in light intensity produced by random movements. Attempts were made to demonstrate the direction theory experimentally. A typical experiment of this type was that of Strasburger (945), made long before Jennings's views were in the field, upon the swarm spores of certain plants. He placed over the vessel containing them an India ink screen, thicker at one end so as to cause gradations in the intensity of the light reaching the vessel. When the light fell perpendicularly through this screen, the distribution of the swarm spores through the vessel was nearly uniform; that is, the differences of intensity had no effect. When the screen was removed, and the light fell at an angle, the spores immediately oriented themselves to its direction, and preserved this orientation even when the screen was replaced. They would move toward the light even when by so doing they passed into a region of less intense illumination.

Jennings argued on the other hand that these results could be explained by changes in light intensity. He suggested that they were due to the fact that "turning the sensitive anterior end away from the source of the light" would diminish the effective illumination of the animal more than passing into a slightly less illuminated region. That is, the two ways of changing the intensity of the stimulus, moving forward into a

darker region, and turning the head end away from the light, are here opposed: the latter effect is stronger than the former, hence the organisms make the negative reaction when the head end is turned from the light, and move toward the shaded region. "If the difference in intensity of light in different parts were increased till the change in illumination due to progression is greater than the change due to swinging the anterior end away from the source of light, then the positive organisms would gather in the more illuminated regions" (512, page 148).

If random movements can be actually observed when an animal is acted on by light, the theory of Jennings receives support. Thus Holmes (460) reports that the negative orientation of earthworms to light occurs by the checking of random movements of the head towards the light. In the crawling movements stimulated when light is thrown upon the worm, the head is turned from side to side. If it happens to be turned toward the light, it is withdrawn. Holmes explains the observation of Parker and Arkin that the head of the worm is much more apt to turn from the light than toward it (761), by saying that account was probably taken here only of the first decided turn made. He himself experimented by lowering a worm, crawling on a wet board, while its body was in a straight line and contracted, into a beam of light at right angles to the body, and noting the first movement of the head. This was found to be twenty-seven times away from the light and twenty-three times toward the light. A similar method of orientation by "trial and error" was observed in the leech and in fly larvæ by Holmes (460). Hess (434) describes behavior in the caterpillars of *Vanessa* that is of this character: they are positively phototropic, and if put down with their tails to the light, they swing the fore part of their bodies for a number of seconds before they turn around. The planarian, when showing negative phototropism, tends to wander to one side or the other: when it has turned its head so far that light enters one eye, it checks the turning (962).

E. H. Harper, on the other hand, working on the earthworm *Perichæta bermudensis*, declares that if the light is strong enough there are no random movements of the head at all; the first movement is a direct reflex away from the light. When the light is only moderate, the appearance of random movements is due to the fact that the worm is less sensitive in a contracted than in an expanded state. Locomotion consists in a series of contractions and expansions, and "as each extension begins in a state of lower sensibility, the anterior end may be projected toward the light, only to be checked when its increase of sensibility with extension makes the stimulus appreciated" (391). A similar suggestion that orientation may occur either by a definite reflex or as the outcome of random movements, according to the animal's physiological condition, is to be found as early as the work of Pouchet on fly larvæ. He noted that the courses taken by the larvæ were either straight, "or they present to right and left indentations due to the wavering movements which the animal makes . . . in a certain number of cases, as if to take at each instant a new direction." These individual differences might have been accounted for, says Pouchet, by differing degrees of hunger in the larvæ (832). Herms (406) reports that to low intensities sarcophagid flies orient by random movements; while to high intensities they orient directly. Bittner, Johnson, and Torrey (73) find that the earthworm orients to light without any random movements. Hadley (372) finds the same true of larval lobsters, Crozier (212) of a holothurian, and Bancroft (25) reports of *Euglena*, a protozoön which has the spiral method of swimming characteristic of so many animals in this group, that "there is nothing of trial and error here: the organism orients as definitely as its spiral locomotion will allow."

The occurrence of "circus movements" in animals with one eye blinded, that is, turning towards the side of the blinded eye on the part of negatively phototropic animals and towards that of the open eye on that of positively phototropic ones, is held to demonstrate the theory of Loeb that the tropism is

due to the relative intensity of light on symmetrical points, in this case the eyes. Patten finds such movements in the whip-tailed scorpion (771), Hartline (395) in isopod crustaceans, Cole (188) in the horse-shoe crab, and Crozier and Federighi (219) in the slug. Garrey (345) gets from the robber fly what he calls convincing proof of Loeb's theory, studying the circus movements made when different halves of the two eyes are blackened.

There are, however, many instances on record of behavior even in quite low animals which cannot be explained on the continuous action theory of Loeb. Taliaferro (962) finds that planarians with one eye removed orient accurately to light, without circus movements. Further, he says, when a planarian is moving away from the light, the eyes, owing to their position, receive no light at all; hence their orientation cannot be due to the action of a continuous stimulation, but may easily be occasioned by the slight changes of intensity in the light stimulus which will occur if the head is moved to one side. Mast (661) says that insects with one eye blinded can often orient accurately. He also (651) challenges the theory of Loeb to explain the behavior he has observed in certain fire-flies, which orient to the flash of another firefly and continue to go towards the same direction after the flash has disappeared. Rabaud (840) asks how unequal stimulation of symmetrical points can explain the turning of an animal whose back is towards a stimulus, through 180° to face it, as is done, for example, by a spider whose web is touched by a tuning-fork? In mayfly larvæ, according to Alverdes (8), there is loss of tonus on the opposite side if one eye is blinded, making the body curve towards that side: in spite of this, the larva can walk straight, compensating by its leg movements for its posture, and is neither positive nor negative to light.

Adherents of Loeb's theory of the tropism argue that when behavior which seems to be inconsistent with the theory occurs, it is due to complicating factors. Thus they criticise Mast's article on photic orientation in insects (661) for failure

to distinguish between leg posture and frequency of leg movements: the orientation of the insect called the water scorpion (*Ranatra*), these critics (220) claim, is produced by the assumption of a different posture on the part of symmetrically opposite legs, though it is true that the rate of movement is the same on both sides. (It might well be replied that a difference in the posture of the legs is harder to explain on the continuous action theory than differing rates of movement). The same critics point out that the orienting reaction of the slug is complicated by the action of two mechanisms, one for turning and one for creeping, whose relation to incidental influences, such as temperature, is different.

Mast (661) urges the following *a priori* argument against Loeb. While light may very well act as a continuous stimulus on plants, whose reactions, such as the bending of a stem towards the light, do not have to be followed by a return to the original condition (that is, are non-reversible), in the case of animals there has to be a period of recovery or restoration. It is therefore probable that even when a visual sense-organ "is continuously illuminated, it is not continuously stimulated"; that is, there are alternating physiological processes of stimulation and recovery.

The conclusion which we may most safely draw from the whole complicated discussion at present is as follows. Those observers who report cases where animals orient to light directly, without any random movements such as the theory of Jennings requires, are too numerous and trustworthy to be disbelieved. Loeb's type of orientation therefore does occur. But the other type also occurs, and by the very nature of the environment of most animals it must be far more frequent than orientation to continuous forces. Loeb himself recognized that change of intensity in a stimulus produces responses, although not oriented responses. Changing stimuli, including changing relations of the organism to stimuli, are certainly the rule, unchanging relations of the organism to constant stimuli the exception, in this changing world. Hence we may well be-

lieve that in the majority of cases, oriented reactions will occur through a physiological mechanism adapted to change of stimulation rather than through one adapted to constant stimulation.

This entire discussion applies not only to light tropisms, but to all oriented reactions, whatever the character of the stimulus.

§ 59. *Influences Affecting the Sense of Light Orientations*

In no class of animal responses to stimulation is the effect more dependent upon the coöperation of a number of conditions than in those involving orientation to light. Many influences have been found to reverse the sense of light reactions, transforming negatively phototropic into positively phototropic animals, and *vice versa*. That such reversal should occur in response to increase or decrease of the *intensity of the light* is what one would naturally expect; if a certain intensity of illumination is favorable to the life processes of an animal, it would seem appropriate for it to seek light of that intensity but avoid light of other intensity. Many animals, like *Gonionemus*, are positive to light of moderate intensity and negative to strong light (1095). The females of the crustacean *Labidocera* migrate to the surface of the water at nightfall because, like the earthworm, they react positively to faint light; and move downward at sunrise because they are negative in their response to intenser light (740). On the other hand, Holmes observed that *Orchestia agilis*, an amphipod crustacean, would, if brought from strong to weaker light, become negative for a short time; the meaning of such a change it is difficult to conjecture (456). Sudden reduction of light causes a temporary negative phase also in *Convoluta roscoffensis* (342).

Adaptation to light may alter phototropism: the "depth migrations," that is, the periodical movements toward and away from the surface of the water, in the free-swimming

larvæ of the barnacle, *Balanus*, are due apparently to the fact that an exposure of several hours of light will make positive animals negative, even though the light at the end of the period of exposure is decidedly fainter than it was at the beginning (366). The positive reactions of the water insect *Ranatra* increase in violence the longer the light acts; on the other hand, after being kept in darkness for several hours, *Ranatra* is negative on first being taken out (461). Exposure to light turns the land crustacean, *Asellus* (the sow-bug) from positive to negative (710).

The colonial protozoön *Volvox* fluctuates from one phase to another under prolonged exposure to light (658). *Daphnias* kept in darkness for a time become decidedly negative to diffused daylight, whereas if kept in light they would have been positive. A sudden change in light intensity, either brightening or darkening, has the effect of making positive *Daphnias* temporarily negative (738).

Temperature changes influence response to light. The obvious suggestion here would be that since increased temperature often accompanies increased intensity of light, animals that are positively phototropic only up to a certain degree of illumination ought to become negative when the temperature is decidedly raised. This, however, is by no means always the effect produced by increased temperature. Strasburger's swarm spores became positive in higher temperatures, negative in lowered ones (945). *Orchestia agilis*, which we have just seen becomes temporarily negative on being brought from strong into weak light, may be made positive again if the water is slightly warmed. When the same animal is dropped into water, it becomes strongly negative, but it will show a positive response if the water is heated almost to a fatal point (456). Essenberg (285) finds that certain aquatic insects are more strongly positive when the temperature is increased. On the other hand, the copepods and annelid larvæ studied by Loeb were made negative by increased, positive by lowered, temperature. Other crustaceans, *e.g.*, *Daphnia* (1101, 250),

had their responses to light unaffected by a fairly wide range of temperature changes.

Mast (657) found that a colonial protozoön would become positive with increase and negative with decrease in temperature. In the slug with one eye tentacle removed, for temperatures above 15° C., increased temperature quickens the rate of turning and slackens the rate of creeping: below 15° the reverse is the case (219).

Increasing or decreasing the density of the water will also affect phototropism. In some copepods diluting the water produced negative responses to light, while increasing its density brought about those of the opposite sign (591). Diluting the water produced negative phototaxis in the larvæ of *Palæmonetes* (619). Parker failed to find any such effect in the case of the copepods studied by him (740). W. Ostwald has called attention to the possibility that "internal friction" between the organism and the medium may affect various tropisms. Freshly caught *Daphnias* which are negative or indifferent, quickly become positive if gelatine or quince emulsion is added to the water. Since they would become so in time anyway, Ostwald thinks the mechanical friction of the sticky liquid simply acts as a "sensibilator" and brings on this positive phase sooner (738).

Change in the purity of the water also sometimes produces change of sign in the response to light. The amphipod *Jassa*, negative in ordinary sea water, becomes positive in foul sea water (456). The *presence of chemicals* is an influence probably identical with the one just mentioned. Various Crustacea have had the direction of their reactions changed by carbonic or other acids, ammonium salts, ether, chloroform, paraldehyd, and alcohol (596). Acids and salts will reverse the responses of May fly larvæ (1083). The ultra-violet rays will make positive *Balanus* larvæ temporarily negative and have a similar effect on *Daphnia* (696).

Mast (657) finds that acids change the phototropism of certain colonial protozoa from negative to positive, an effect

probably due to the reduction of hydroxyl ions in the culture solution: anesthetics produce the same reversal. Kanda (530), working with the larvæ of a marine worm, gets reversals from various salts, esters, and acids, and suggests that they act by affecting the plasma membrane.

The state of hunger or satiety in an animal must be reckoned with: the caterpillars of *Porthesia*, for example, are decidedly positive when hungry, much less so when fed (589). The horse-shoe crab loses its phototropism when hungry (188). The slug *Limax maximus*, ordinarily negative to strong light, is positive to light of any intensity when hungry (314).

Closely related to this factor is probably the *rate of metabolism*. Allee and Stein (5) measured this for May-fly nymphs by their resistance to poisoning by potassium cyanide: the longer they survive, the higher their rate. When the phototropism of these insects was reversed by the action of various chemicals, their metabolic rate was always markedly affected, whether raised or lowered: changes in metabolic rate were not always, however, accompanied by reversals of phototropism.

Mechanical stimulation is most striking in its effect on light reactions. Pouchet in 1872 noted that fly larvæ after having been shaken fail to display their usual orientation to light (832). The copepod *Temora longicornis*, usually negative, can be made positive by shaking it (591). Very curious phenomena of a similar nature have been observed in the case of some Entomostraca. Certain individual specimens of the ostracod *Cypridopsis* appeared to be decidedly positive, others negative. Careful experimental analysis of the conditions revealed the following as the true state of affairs. The animals are predominantly negative. But contact with a mechanical stimulus has the effect of making them positive; thus a negative animal that is picked up in a pipette, or merely comes in contact with the end of the trough in swimming away from the light, may become positive. In course of time such a positive animal will become negative of its own accord, so to speak,

without further mechanical stimulation, but such stimulation, if applied, makes it negative at once (979).

Similar experiments upon *Daphnia* and *Cypris* gave results of the same general character. The strong positive tendency of the former may, by several times taking the animal up in a pipette, be made very temporarily negative; the opposite effect could not be well tested because of the difficulty of preserving the negative state long enough to experiment on it. In the case of *Cypris*, an individual temporarily negative could be made positive by picking it up, but the positive phase could not be similarly reversed. No other sudden stimulus produces the effect which is thus induced by mechanical contact (1093).

The effect of contact was observed by Holmes in the terrestrial amphipod *Orchestia agilis*. The most permanent phase of these animals is positive, although they are at rest under seaweed on the beach by day. But when they are thrown into the water, they become strongly negative, no matter what the intensity of the light; and to a considerable extent this effect is independent of the temperature (456, 125). In the case of the copepod *Labidocera æstiva*, being picked up in a pipette will make the females, ordinarily positive, negative for a time. The males are normally slightly negative, but picking them up, instead of reversing this tendency, increases it (740). The strong positive phototropism of the "water scorpion" *Ranatra*, an hemipterous insect, may be made negative by handling, and especially by dipping in water (461).

Periodical changes in the sense of response to light have been observed in animals subjected to periodical changes in environment. The gasteropod mollusk *Littorina* lives on the rocks of the seacoast in regions where it is covered with water at high tide and exposed to the air at low tide. According to the height at which they are found, some of these animals undergo the alternations of wetness and dryness at the ordinary tidal periods, twice a day, while others are reached by the water only at the special high tides occurring every fourteen

days. Mitsukuri showed that when the waves of a rising tide cover these mollusks, they display negative phototropism and seek shelter in rock cavities; while as soon as they are again exposed to the air, their phototropism becomes positive and they emerge in search of food. Further, he found that a *Littorina* whose phototaxis was negative could be made positive by being subjected to the action of a stream of water for a time (690). Bohn later studied the effects of placing black or white screens near the animals at various angles to their crawling movements, and found that the black screens exerted an attractive influence at certain times, the white screens at others. These changes in the "sense" of the phototropism correspond in time to the oscillations of the tide, even though the animals are studied in the laboratory; they tend gradually to grow less pronounced, however, under such circumstances. Further, the level from which the *Littorinas* are taken influences the nature of their response to light. Those from high levels, "which undergo prolonged and intense desiccation, habitually move following the direction of the luminous field in the negative sense; the *Littorinas* from low levels, which undergo only short and slight desiccation, move, habitually, following the direction of the luminous field in the positive sense." The former become positively phototropic at the time of highest water, the latter negatively phototropic at the time of low water. In all cases, the tendency is for the animals to become negative at low-water time. The attraction of the dark screens represents that of the dark surface of the rocks (96). Similar oscillations corresponding to the periodicity of the tides were observed in the annelid *Hedista diversicolor* (96), in the sea-anemone *Actinia equina* (81), and in the hermit crab (262, 263).

It is probable that such rhythmic changes in the sense of light response are due to the effect of a rhythmically recurring cause, such, for instance, as the mechanical disturbance caused when the waters of the rising tide begin to agitate the pool in which the animal dwells, or to the *wetness* or *dryness*

of the tissues. Bohn has suggested this explanation for the oscillation of *Hedista*, just mentioned. He supposes that when the annelid is dry, light has the power of exciting muscular movements, that is, a kinetic effect. This means that when the worms have accidentally crept into the shade they come to rest. If one eye has its illumination diminished, there is an inhibition of muscular activity on that side, and consequently a turning in that direction. At the period of high tide, when the muscles are wet, the action of light on the animal is inhibitory and the above phenomena are reversed (96). Heat and dryness make terrestrial amphipod crustaceans positive to light; cold and wetness make them negative (125).

The *state of rest or movement* is still another factor. The "mourning cloak" butterfly, *Vanessa antiopa*, on coming to rest in bright sunlight, orients itself with the head away from the light. When it moves, on the other hand, it flies toward light of any intensity (743). Bohn also has noted that certain butterflies orient themselves when alighted in such a way that the posterior part of the eyes is toward the light. When in this position there is a tendency for the wings to be spread apart, while when the insect is facing the light the wings are closely folded (98). The effect on the wings was noted in *Vanessa* also, and, it is suggested, may have some function in bringing the sexes together (743). The pomace fly when at rest is not oriented at all. Light exerts upon it merely the effect of stimulating it to movement, a kinetic, not a directive, effect. When the movement has been started, however, it is directed toward the light. But owing to the kinetic influence of the light, when the insects have been long exposed to sunlight they tend to come to rest in the more shaded portions, with their heads away from the light, for this is the position in which they are least stimulated to movement. The kinetic effect increases with the intensity of the light, but its directive effect, through which orientation is secured after the movement is started, was at least in one case lost under intense light (154). Brundin (125) has suggested that the effect of mechanical stimulation

in reversing light reaction may be due to the state of activity it induces.

The *background* sometimes determines the sense of the reaction. Keeble and Gamble found that while the crustacean *Hippolyte varians* would move toward the light whether it was on a white or black background, *Macromysis inermis* was negative on a white ground and positive on a black ground (534).

In the horse-shoe crab, and probably in other animals, phototropism may be inhibited by fright, by photokinesis, by stereotropism, and by "unknown stimuli" (188).

Despite all this complex influence of external and internal conditions on phototropism, that it is based on innate factors is indicated by observations on the fruit-fly, that creature indispensable to the student of heredity, in which responsiveness or indifference to light seems to be inherited along with certain differences in pigmentation: a "tan" fly, for example, is regularly indifferent to light (626). An interesting problem is presented by the seashore mollusk *Onchidium*. When seeking food on the rocks near its home, it makes no adjustment to light whatever; but when transferred to the laboratory, or even moved to another locality on the shore, it shows decided negative phototropism. The familiar contact stimuli about its home inhibit its phototropism, it is argued, and so the phototropism is really useless, an example of many useless innate endowments of animals (11). One may conjecture, however, that negative phototropism might actually be of service to these animals when swept away from their normal range, as it would lead them to seek concealment.

§ 60. *The Psychic Aspect of Orientation to Light*

The behavior of an organism which, by the unequal contraction of symmetrically placed muscles, is forced around into a position directly facing or turning tail to light, the light acting as a continuous stimulus and not through changes in intensity, is without any parallel in human experience, and hence

suggests no psychic accompaniment. Yet there seems to be a considerable amount of evidence that such a type of reaction does occur, given the proper amount of stimulus and the proper physiological condition in the animal. It is a fact of much interest, however, that when we reach organisms beyond a certain point in the ascending scale of complexity, the tropic type of response to light begins to give place to more variable responses suggesting analogies with our own behavior. The individual experience of an animal strongly modifies its tropisms, as we shall see in a later chapter. Brundin (125) says that in certain amphipod crustaceans which he studied, the "mode of behavior exhibits a transition from the stage at which the creature is at the mercy of its environment to a stage at which it is beginning to hold its own against the forces which have shaped it." Quite possibly, however, the ability to modify tropic response by individual experience is found in all animals, and not merely in those above a certain stage; it does seem to be true, though, that the tropisms are more readily overthrown by other influences, the higher the animal. Thus Holmes (463) says of fiddler crabs that phototropism is easily overcome by fear; although they are strongly positive they will run away from a moving light. "Light," he says, "is followed much as an animal pursues any other object of interest"; and Turner (993) has made similar comments on the behavior of certain insects to light. Bohn says of the mollusk *Littorina* that when its tissues are neither very wet nor very dry, it ceases to respond with a fatal necessity to light; "the animal seems, as it were, to disengage itself from the influence of external forces, seems no longer to behave like a pure machine: it goes to the stones and seaweed where it may find shelter and nourishment as if it saw and was conscious of them" (96).

Kühn (564) has suggested the following terms: *tropotaxis*, when equal stimuli fall on symmetrical points, causing symmetrical nerve excitations and muscle tensions, so that the animal follows a diagonal between them; *menotaxis*, when an animal receiving unequal stimulation of symmetrical

points compensates for this and continues on its original course; *telotaxis*, when the animal chooses one of two lights and goes towards it, instead of following a diagonal between them; *mnemotaxis*, when the reaction is modified by learning. These evidently represent increasing degrees of emancipation from the tropism. It must be noted that when we speak of an animal's being emancipated from a tropism, or not behaving like a pure machine, we are not for a moment implying that its actions will not some day be explained on physico-chemical grounds; we are not abandoning mechanism in favor of vitalism.

The development of the visual image of course profoundly modifies the oriented response to light. The crawling of newly hatched loggerhead turtles towards the sea, believed to be aided by positive geotropism, has been shown by Parker (758) to involve another factor. They tend to move towards "regions in which the horizon is open and clear, and away from those in which it is interrupted." When they were placed on an inverted tub, they made, no matter in what position they were set, a preliminary circling movement with head in the air, and then set off in the direction of the most open horizon, which would ordinarily be the direction of the sea. Hooker (471) thought they moved towards masses of blue, and thus towards blue sky and sea; on either hypothesis, as Parker says, they cannot be appropriately called either positive or negative to light, but respond to the details of their retinal images.

§ 61. *Mutual Influence of Light and Gravity Orientations*

Orientation to light and orientation to gravity are not without mutual influence in determining the behavior of an animal. Supposed instances of this have been noted in the case of the periodically changing geotropism of *Convoluta roscoffensis* (342) and in the copepods observed by Esterly (286). The relations of gravity and light responses in the larvæ of the squid, a cephalopod mollusk, seem to be as follows. The

larvæ have a tendency to rise to the surface of the water both in darkness and in light, suggesting negative geotropism. Two test tubes were arranged by Loeb, one lying horizontally and at right angles to a window, the other inclined at an angle of 45 degrees from the upright position, and with the upper end directed away from the window. Larvæ were placed in both tubes; those in the former showed positive phototropism by collecting at the end nearest the window, but those in the latter gave evidence that their negative geotropism was stronger than their positive phototropism by rising to the upper end, although it was farthest from the source of light (594). It is not usual for geotropism thus to come off victorious in a contest with other stimuli. Jennings says, "As a rule, the reaction to gravity is easily masked by reactions to other stimuli" (512, p. 150). In the mollusks observed by Bohn, the tendency in ascending or descending the rocks is to orient the body in the line of the greatest slope. When light and gravity are acting together upon the animal, its movement seems to be a resultant of the two, but if the mollusk is made to move on a vertical plane, gravity thus exerting its maximal force, the influence of the light disappears altogether; and if the animal is put in an upside-down position by further tipping of the surface, the sense of its phototropism is reversed; that is, it may be repelled instead of attracted by a dark screen (98). The fairy shrimp, *Branchipus*, is positively geotropic in light, negatively geotropic in darkness (627).

The geotropism of the planarian is affected by previous exposure to light (732), and the phototropism of the Japanese beetle is shown in hastening the insect's negatively geotropic movements when it is illuminated from below (699).

A curious tendency has been noted by many observers in insects with both eyes blinded; namely, to fly straight up into the air. Forel thought they did so because in no other direction could they escape obstacles (308); but this fact they would have to learn by experience, for which, in some

cases at least, they do not take time. Plateau believed the rising into the air was due to sensations produced by the action of the light on the surface of the body, leading the insects in the direction of the strongest light, which usually comes from above. He supported this view by showing experimentally that a blinded insect would not rise if set free at night, while on the other hand, if liberated in a lighted room, it would, in spite of the blinding, fly toward the light or the lightest part of the ceiling (812, 815). In the butterfly *Vanessa*, Parker thinks the rising due to negative geotropism, as the insect flew upward in a darkened room (743). Axenfeld suggested that it might be caused by light penetrating the integument of the head (17).

§ 62. *Orientation to Other Forces*

One force, which, as was noted in Chapter III, produces orientation, namely, the electric current, we shall leave out of account. It is not a stimulus to which animals are normally subject, and though its action on living matter is of great interest to the physiologist, the comparative psychologist's difficulty in finding a psychic interpretation for the facts may justify setting them aside. Similar considerations apply to orientation to centrifugal force. There remain the orientations that have been termed respectively "rheotropism" and "anemotropism," responses to currents of water and to currents of air.

The tendency shown by many aquatic animals to orient themselves with head up-stream, and to swim against the current, was formerly thought to be a response to the pressure exerted by the current—a reaction leading the animal to resist pressure. Lyon, however, pointed out that this explanation assumes rheotropism on the animal's part. It is because the animal opposes the current that the current exerts any pressure. If it merely allowed itself to be carried passively along, and if the current surrounding the animal

flowed with uniform velocity in all its parts, no stimulus whatever could be exerted by the water pressure (616). It seems probable that eyeless animals do not, as a matter of fact, orient themselves against a current of this sort, and that rheotropism in their case occurs when a current of unequal velocity disarranges their movements, or when they are in contact with a solid body. Thus Jennings has suggested that in *Paramecium* the reaction is due to the fact that unless the animal has its head to the current, the flow of the latter will interfere with the normal backward stroke of the cilia, causing negative reactions until the disturbance is removed by proper orientation (512, p. 74). Planarians living in swiftly moving streams orient themselves so that the head receives the strongest pressure and the stimulation of symmetrical points is equal. Where two streams join they creep against the swifter (255).

In animals with eyes, there is reason to think that apparent rheotropism is largely an affair of vision. Lyon's theory of rheotropism in fishes is that the fish orients itself and swims in such a way that its surroundings, the bottom of the stream, for example, shall appear to the sense of sight to be at rest, an hypothesis which, as we shall see, was adopted by Rádl to explain the "hovering" of insects in one place (842). Lyon supports it by experiments where the bottom or sides of the aquarium were caused to move in the absence of any current in the water, and the fish was found to follow them. When the fish was placed in a revolving glass cylinder, it followed the revolutions, although there was a slow current, of course, in the same direction, against which, on the pressure theory, the fish should have moved. Still more decisive was the experiment where young fish were placed in a corked bottle full of water which was submerged and put near a wall covered with algæ. When the bottle was moved in one direction all the fish went to the opposite end, although no current could have been produced. Again, a wooden box with ends of wire netting, the bottom covered with gravel and

the sides with seaweed, was used; fish (*Fundulus*) were placed in it, and the box was held lengthwise in a strong current. The fish oriented themselves, but as soon as the box was released and allowed to float away, they lost their orientation, though their relation to the current was in no way altered. Blind fish, Lyon found, oriented themselves by touch, sinking to the bottom. There does, however, appear to be, in some cases, a genuine pressure reaction to current, for when water is rushing through a small hole into a tank containing blind fish, they keep their heads to the current without touching anything. Here the different parts of the stream have different velocity, and pressure stimuli are actually applied to the skin. There must be pressure reaction, also, when fish actually swim up-stream instead of merely maintaining their places against a current (370). Such a reaction was displayed, probably, by some shrimps which, being in the water with the fish in the revolving tank experiment, did swim against the current instead of with it (616).

Oddly enough, one small fish orients itself with its tail rather than its head to the current, and Jordan (521) says this reaction is really a negative one to stimulation of the lips by the current. The body orientation may be thus explained, but of course the true rheotropism, the resistance to being swept away by the current, must be already in operation or the current would not stimulate either lips or tail.

Some very interesting behavior touching on this same point was observed by Garrey in a school of the little fish called sticklebacks. He noted that if any object was moved along the side of the aquarium containing them, the whole school would move along a parallel line *in the opposite direction*. If an individual fish happened to be heading directly toward the object, it would turn in the opposite direction from the one in which the object was moved; if it was heading somewhat in the opposite direction already, it would turn farther in that direction until parallel with the object's line of motion; if it was heading somewhat in the same direction as the

object, it would "back off hesitatingly," and reverse itself by a turn in either direction, usually taking the way around toward which it was already partially headed, if the object was rapidly moved, but the other way around if the object's motion was slow. At first sight this behavior seems to display an instinct precisely opposite to that of keeping the visual field constant. Yet the sticklebacks, when placed in a cylindrical glass tank inside of a black and white striped vessel, moved with the latter when it moved, proving that they possessed the usual tendency shown by Lyon to be involved in rheotropism. Garrey points out that movement in the opposite direction is produced not when the whole visual field moves, but when it is at rest, and one object in it moves. Can it be, he asks, that the moving object "fixes the attention" of the fish and produces an apparent motion of the background in the opposite direction, which motion the fish follows? (343).

Rheotropism in water arthropods may be similarly accounted for, and in the opinion of Rádl, this same tendency explains the habit swarms of insects have of hovering over the same place, a phenomenon which Wheeler thought might be due to odors emanating from the soil (1064). Insects will often be found to follow an object over or under which they are grouped in the air, if it be moved (842). Swarms of insects may be noted in the air over a country road, following its windings and apparently oriented by the contrast between the road and the dark banks on either side. When, however, resting insects turn so as to keep their heads to the wind, the reaction is evidently really due to the wind and not to their visual surroundings (878). Probably the disturbance to their wings produced by any other position causes them to rest only in the "head-on" orientation. The fruit-fly resists air currents, Cole thinks, as a result of their stimulation of the leg muscles (186).

The responses of animals to different intensities of *heat* seem not to involve a definite orientation of the body. A

temperature above the optimum produces wandering movements, which cease when the animal happens to reach the proper temperature (670, 673, 1101).

§ 63. *Class III: Reactions to a Moving Stimulus*

Specialized response to a stimulus in motion, that is, one which successively affects several neighboring points on a sensitive surface, is also frequently met with in animal behavior. Its usefulness is obvious: a stimulus in motion is very commonly a living creature, hence either an enemy or food. In any case it must be reacted to with extreme promptness. Reactions of this class may be distinguished as tactile or visual according as the moving stimulus is mechanical or photic.

We find good examples of specialized reactions to *motile touch* in the cœlenterates. The sea-anemone *Aiptasia* gives its most violent reaction, involving all the tentacles at once, when touched by a moving object (721). The medusa *Goniomemus* makes, in the case of a moving mechanical stimulus, its single exception to the rule of responding by the feeding reaction to edible substances only. The tentacles are wound corkscrew fashion about a glass rod drawn across them, they bend in toward the mouth, and the bell margin bearing them contracts; the feeding reaction goes no further, however. But the response is differentiated from that to any other form of stimulation by its greater speed; the reaction time is from .3 to .35 of a second, compared with .4 to .5 of a second for other stimuli (1095). Special vigor and speed generally characterize reactions to contact with moving objects. In eliciting the scratch-reflex of dogs, an object drawn along the skin is decidedly more effective than one pressed against the skin for the same length of time (928, p. 184). The physiological effect is probably, Sherrington says, the same as that involved in the "summation" of successive slight stimuli applied at the same point. As is well known, the latter will

bring about a response of considerable violence, though each stimulus acting alone would apparently be without effect.

Is it likely that these responses to moving stimuli in contact with the skin involve the perception of movement as a form of space perception; that is, a perception of the successive positions occupied by the stimulus and their relative direction? I think we may say that they probably do not, in the lower animal forms at least. And a chief reason for saying so lies in the fact that the reactions are so rapid. To perceive the spatial relations of stimuli, or any other relations, is a process not favored by great speed of response. The quicker the reaction, the less clear the perception of its cause: such seems to be the general law. The sensation accompanying contact with a moving object may differ in intensity from that accompanying a resting stimulus; it may, in the lower forms, differ qualitatively in some way not represented in our own experience, but it can hardly be connected with the more complex psychic processes involved in any form of space perception.

In vision, also, there are special arrangements for reacting to moving stimulation. The sensitiveness of many animals to changes of light intensity, although not a direct adaptation to the spatial characteristics of a stimulus, serves the same purpose, for changes in light intensity are oftenest brought about by objects in motion. In the mollusk *Pecten varius*, a transition from shadow vision to movement vision is illustrated: the animal closes its shell when a shadow is moved so as to fall on its eye spots in rapid succession (848). Generally speaking, the simple invertebrate eye, however, is adapted to respond to changes in light intensity rather than to moving objects. Plateau found that caterpillars, which have only simple eyes, could see moving objects no better than those at rest (813), and Willem was inclined to think snails saw resting objects better than moving ones (1074). On the other hand, the compound eye (see page 214) is specially formed to be affected by moving stimuli. The cray-

fish will react to anything of fairly good size in motion, but is apparently unable to avoid stationary objects in its path (49). The poor vision of the compound eye for resting objects is shown by the ease with which insects may be captured if the movements of the captor are very slow. They may be readily approached, also, if the movements are all in the line of sight, that is, directly toward the insect, so that successive facets of the compound eye are not affected, as would be the case in lateral movements. Let the reader try bringing the hand slowly straight down over a fly, and see how much closer he can come before the fly is disturbed than he can if the hand is moved from side to side. Plateau, from experiments on different orders of insects, concludes that "visual perception of movement" is best developed in the Lepidoptera (moths and butterflies), Hymenoptera (ants, bees, and wasps), Diptera (flies), and Odonata (dragon-flies); that the distance at which movements can be seen does not exceed two metres, and averages 1.5 metres for diurnal Lepidoptera, 58 cm. for Hymenoptera, and 68 cm. for Diptera (815).

Chicks proved to have good visual perception of the rate of movement, as measured by their ability to distinguish the flickering of interrupted light from that produced by twice as frequent interruption (72). Rats, which by all evidence are far less "visual" in their type than fowls, took on the other hand about seven hundred trials to distinguish a moving light from a still one (852). And dogs, also little inclined to the use of sight, failed almost completely to distinguish a pair of white disks at rest from a rotated pair, one being the sign of food and the other of electric punishment (958).

End. Feb. 1911

CHAPTER IX

SPACE PERCEPTION AND THE PERCEPTION OF THINGS

§ 64. *Class IV: Reaction to an Image*

By an image is meant the perception of simultaneously occurring but differently located stimuli as having certain spatial relations to each other. Through its means, or that of the nervous processes underlying it, there arises the possibility of adapting reaction not merely to the location of a single stimulus, but to the relative location of several stimuli. Responses may thus be adjusted not only to the direction of an object but to its form. On the basis of such adjustments a whole new field of possible discriminations is opened up.

The commonest arrangement for the production of a visual image is the double convex lens, which collects the rays of light diverging in their reflection from an object and brings them together again upon the sensitive retina. The lenses found in many simple invertebrate eyes seem, however, very ill adapted to the image-producing function. It is probable that they serve rather to intensify the effect of the light rays by bringing them together, than to give a clear-cut image (723). In the eye of certain invertebrates, such as the Nautilus, a cephalopod mollusk, while there is no lens, the opening admitting the light rays is so small that an inverted image might be formed through it, such as may be obtained through a pinhole. It is unlikely, however, that this eye is really an image-producing organ. Hesse includes under image-forming eyes only the camera or convex-lens eye, the mosaic eye, and the superposition eye. The last is a peculiar form of compound eye where light can pass from one section

to another, and where the image is formed by the coöperation of various refracting bodies (448).

The simplest and vaguest conceivable visual image would be that of a visual field whose different parts should differ in brightness. An eye capable of furnishing indications merely of the direction from which the greatest illumination comes



FIG. 11.—Diagrammatic representation of the compound eye of a dragon-fly. *C*, cornea; *K*, crystalline cone; *P*, pigment; *R*, nerve rods of retina; *Fb*, layer of fibres; *G*, layer of ganglion cells; *Rf*, retinal fibres; *Fk*, crossing of fibres. After Claus.

might produce this kind of an image, which would of course not allow the perception of objects, only that of brightness distribution. The compound eye found in crustaceans and insects would seem to be adapted chiefly for the perception of light direction and of moving stimuli.

It consists essentially of a number of simple eyes so crowded together as to produce a common faceted cornea, each facet belonging to an eye. These facets are lens shaped, and back of each lies a refractile crystalline cone. Behind these, in turn, are nervous structures, the rods or retinulae, each separated from its neighbors by a pigment sheath. Light rays passing through each corneal facet probably produce a single spot of light on the retinula, and the total image may thus be a mosaic formed of these spots (Fig. 11).

We have already seen that the orientations of certain ani-

mals to light seem to be produced through a tendency to take such a position that the two eyes shall be equally illuminated. If the two visual fields are combined in the case of such animals, as they are in our own binocular vision, under ordinary conditions the oriented position would give a field whose brightness is uniform throughout, while any other position would give greater brightness at one side of the field. If they are not combined, if there is no binocular vision, we cannot imagine what the resulting perception is. In the case of the starfish, we have an animal which seems to "see" a vertical white wall or dark wall that does not cast any actual shadow upon it; the starfish will direct its movements to or from such objects. Since the starfish has only eye-spots on the tips of its arms, with no arrangements for the formation of an image, and since the eye-spots are not arranged close enough together so that differences of illumination in different parts of a field could be represented by the different illumination of different eye-spots, we can explain the reaction to walls only, as Cowles (209) does, by supposing that those eye-spots and portions of the body nearest, say, a white wall, are more strongly illuminated than those furthest away. The response would then be one to different intensities of stimulation on different parts of the body, and these differences would not be seen as composing a visual field.

That the direction from which the light comes influences ants in finding their way is the opinion of Lubbock (609), Turner (988), and Santschi (892). The first named found that ants which had learned the way back to an artificial nest were confused when two candles which had stood near the nest were moved to the opposite side. Turner made a similar observation, and Santschi suggests that the compound eye may perceive the direction of light by acting as a kind of sundial. He was able to make ants reverse their course when he altered the light direction by the use of mirrors.

§ 65. *Methods of Investigating the Visual Image*

Various methods of solving the problem as to the nature and accuracy of an animal's visual images have been used. One method consists in a study of the sense-organ itself, removed from the body. For example, Petrunkevitch (789) has thus investigated the sense of sight in spiders. These animals do not have the compound eye, but a number of simple eyes placed in groups. By a careful measurement of the possible minimal angles of vision in two spiders, *Phidippus* and *Lycosa*, the conclusion is reached that while a creeping insect about one square centimeter in size would be to the human eye so clearly visible at a distance of three meters that its species could be recognized, it would be only an indefinite moving speck to the eye of *Phidippus* and wholly beyond the range of vision of *Lycosa*.

Again, inferences are drawn as to the visual powers of animals from miscellaneous peculiarities of behavior. Thus Petrunkevitch (790) reports that a male spider of the species *Dysdera crocata*, in the courting stage, "watched" the movements of the end of a hatpin with which the observer was breaking clumps of earth, and when the movement ceased the spider approached the spot and scratched it with his front legs. The sight of a female spider digging had the same effect upon him, so evidently the visual image which he received was hardly more definite than one of general size and movement. Bauer (37) reports of the mollusk *Pecten*, which has eyes of peculiar and complicated structure, that when a small quickly moving shadow is cast upon it, the tentacles are quickly withdrawn; large or slowly moving shadows have no effect, but a small, slowly moving shadow makes the animal stretch its tentacles and eyes towards the shadow. In this way, Bauer thinks, it is enabled to ascertain the nearness of its worst enemy, a starfish: apparently he supposes that the movement of the eyes towards the shadow gives an opportunity for visual perception of its form or characteristic

movements. Wenrich (1059) has recently obtained the following evidence of the formation of an image in Pecten. The bivalve normally responds only to a decrease in illumination, not to an increase. If a white card is moved across a black one, the card being not less than fifteen millimeters square and its distance not greater than thirty-five centimeters, Pecten responds by closing its shell, although the illumination is increased rather than diminished.

The chief lines of evidence, however, from which the nature of the visual image can be concluded are three: experiments on the visual perception of size, experiments on the visual perception of form, and experiments or observations on the recognition of visual landmarks in homing.

§ 66. *The Visual Perception of Size*

Bohn's observations on the mollusk *Littorina* show that its reactions are influenced by the size of the illuminated or darkened surface, as well as by the intensity of the light. When neither very wet nor very dry, *Littorina* will react to small objects in its neighborhood, whereas in an extreme state of "hydration" or desiccation it responds to the attraction or repulsion of the larger screens with fatal uniformity (98).

Plateau attempted to test the responses of certain *Diptera* to the size of an opening admitting light, by placing them in a dark room, into which light entered from two sources. One was a single orifice large enough to let the insects out; the other was covered with a net whose meshes were too fine to allow them to pass. The amount of light from the two sources could be made equal. When this was done, the insects, which were positively phototropic, sought the two equally often; if the light from either was made more intense, they went to that one. Plateau concluded both that the flies could not see the netting and that the area of the light source did not affect them (808). On the other hand, Parker found that the mourning-cloak butterfly did discriminate areas,

flying to the larger of two sources of equally intense light (743).

This method of testing the image-forming power of an animal's eyes has been elaborated by L. J. Cole. He subjected animals with decided positive or negative phototropism to the influence of two lights made equally intense but differing in area, one coming through a piece of ground glass 41 cm. square, the other a mere point. Eyeless animals, the earth-worm, for example, reacted equally often to each light. Animals whose eyes from their structure have been judged capable of perceiving merely the direction of light rays, such as the planarian *Bipalium*, confirmed the argument from structure by showing little more discrimination than the eyeless ones. On the other hand, animals with well-developed compound or camera eyes, for example certain insects and frogs, did distinguish between the lights, going, if positively phototropic, toward the one of larger area; if negatively phototropic, away from it (178).

Cockroaches could not learn to distinguish between two lighted areas of equal intensity, one 3 cm. in diameter and the other 12 cm.; they did display, however, some tendency to prefer the smaller area, and since they are negatively phototropic, this preference indicates a vague perception of the difference in size (273). Turtles showed remarkable keenness of discrimination in the study made by Casteel (165), in which they were offered the choice of two compartments faced with cardboards carrying black lines on a white ground. Two turtles learned to discriminate between vertical lines 8 mm. in width and vertical lines 2 mm. in width; and one gifted animal learned to distinguish, first, lines 8 mm. wide from lines 1 mm. wide, then between a width of 4 mm. and a width of 1 mm., then between 4 and 2 mm., and finally between 3 and 2 mm. Chicks proved equal to a discrimination between a standard circle 6 cm. in diameter and one from one-fourth to one-sixth larger. The relative brightness of the circles was varied so that the chicks could not use this as a

basis for their choices (119). Riekel (866) reports that fowls can compare the size of areas, but not the length of lines: this is evidently a matter concerning their power of analysis of their environment (see § 72).

Revesz (859) has ingeniously shown the presence of a familiar illusion of size in the case of fowls. They were trained to peck at the smaller of two circles strewn with food; this training was effective in making them peck at the smaller of two triangles, squares, or parallelograms. They were then confronted with two similar and equal segments of a circle, the upper sides being arcs of a large circle and the lower sides arcs of a small circle: when one of these segments is placed above the other, the larger arcs being uppermost in both cases, there is to the human eye the illusion that the lower segment is larger than the upper. The fowls betrayed the presence of the same illusion by pecking at the upper segment.

White rats can discriminate circles 30 mm. in diameter from circles 50 mm. in diameter, and squares 12 cm. a side from squares 1 cm. a side (411). Discrimination of boxes differing in size but alike in form, placed in a row along a board, food having been put in one, was imperfectly learned by two *Macacus* monkeys (571). Raccoons were taught to distinguish perfectly between two cards, one $6\frac{1}{2}$ inches and the other $4\frac{1}{2}$ inches square, shown successively: the animals had to climb on a box when the larger card was shown and to stay down when the smaller one appeared (180).

One apparent effect of size upon visual perception relates to the distance at which an object produces a reaction. Caterpillars, for example, are described as giving evidence of seeing a slender rod extended toward them at a distance of about a centimeter; large masses they reacted to at somewhat greater distance (813). It is highly doubtful whether this means that the simple eye of the caterpillar could give a perception of two objects as differing in size if they were equally distant. Myriapods, which make very little use of

sight and do not perceive their prey until they touch it, give evidence of seeing an obstacle having a rather broad surface, the size of a visiting card, at a distance of about 10 cm., if it is white and reflects much light, or if it is blue; but not if it is red. Snails can move to avoid objects 10 cm. away (132).

§ 67. *The Visual Perception of Form*

The second method of studying visual images tests an animal's power to discriminate *forms*. Bumblebees were thought by Forel to evince a capacity to distinguish a blue circle from a blue strip of paper when they had previously found honey on a blue circle, even though the two had been made to exchange places. They flew first to the place where the blue circle had been, but did not alight upon the strip. Wasps also, according to Forel, distinguished among a disk, a cross, and a band of white paper, going first to the form on which they had last found honey (308). Turner (991) reports the ability of the honey bee to distinguish, in the open air, among "artefacts" of various forms (disks, cornucopias, and boxes), covered with various patterns such as transverse and longitudinal stripes, mottled surfaces, and spotted surfaces; if the bee had found honey in an artefact of a certain pattern it would select that pattern from among other patterns or plain colors. Von Frisch (327) finds that bees can discriminate patterns like those of flowers, but fail with those very unlike flower patterns; and Knoll (544) by experiments with butterflies has convinced himself that they recognize artificial forms and spots, and by similar marks are enabled to find honey quickly in various kinds of flowers. This evidence, taken at its face value, indicates that the compound eye is able to furnish a fairly clear image, and not merely discriminations of light direction and movement.

Among vertebrates, Parker's (758) observations indicate, as we have seen, that young loggerhead turtles first find the sea by going towards that part of their visual field which

shows least detail. Various species of birds were experimented on by the method of placing cards carrying simple designs over glasses covered with grey paper, food being found always under the same card. The English sparrow and the cowbird both learned to distinguish a card bearing three horizontal bars and one bearing a black diamond from each other and from plain grey cards. On the other hand, the sparrow, curiously enough, did not succeed in discriminating vessels of different form; the cowbird was not fully tested with these, but gave some evidence of learning (828, 829). Pigeons were only moderately successful in a similar test (882). Breed (118, 119) and Bingham (70) investigated the form discriminations of the chick, using the more accurate method of offering a choice between compartments illuminated through openings of different forms. One out of three of Breed's chicks succeeded in discriminating between a circle and a square: Bingham's chicks distinguished between a circle and a triangle when the apex of the triangle was on top, but the discrimination broke down when the triangle had its base uppermost. Form is less readily discriminated than size by the chick (72). The most careful work that has been done on the discrimination of forms or patterns by animals is that of Johnson (519). His apparatus allowed the presentation of two illuminated fields whose intensity could be perfectly controlled, with black bands across them whose width could be varied at will. He proposed four problems: (1) the width of stripes necessary to make a striped field just distinguishable from a uniform field; (2) the just noticeable difference between the width of stripes on two fields; (3) the just noticeable difference in the direction of the stripes on two fields; (4) the just noticeable difference in brightness between two fields, one of which has stripes of equal brightness, while the stripes on the other are of unequal brightness. The chick's ability to distinguish a striped from a plain field proved to be about one-fourth that of a monkey or human being; when the problem of distinguishing between striped fields whose stripes

were of different widths was presented, the monkey did ten times as well as the chick. For differences in the direction of stripes, the threshold of the chick was between twenty-five and thirty degrees; the monkey's was between two and five degrees: moreover, the monkey learned the discrimination in twenty trials, while the chick required 585. It seems practically certain that the chick is not a fair representative of the bird family as regards the clearness of its vision for form and size; the eye of a hawk is a proverb for keenness, and the ability of birds to find their food by vision demonstrates the high development of their eyes in image-forming power.

Among mammals, many dogs have been taught to distinguish printed letters on cards: Sir John Lubbock's poodle "Van" is a familiar example. Van learned to pick out cards marked "Food," "Bone," "Out," "Water," and the like, and to present each on its appropriate occasion (613). Such observations, however, are very inconclusive when compared with modern experimental studies where all the sources of error, from smell, for example, are carefully controlled. In Johnson's (519) study of the visual acuity of the dog, while two chickens and a monkey learned to distinguish a striped from a plain field in from three hundred to four hundred trials, dogs failed to learn in over a thousand trials, although the stripes were made nearly six times as wide. The dog could not distinguish between two visual fields unless they differed in intensity. Thus his visual images would seem to be far from clear. The eye of the dog, it may be noted, like that of all other mammals save the primates, has no fovea. Johnson thinks the dog's vision is used chiefly for the perception of moving objects. Szymanski (953) finds that when dogs and cats have been trained to go to a box in a certain corner to get food, and the box is moved, the dogs show their lack of dependence on vision by displaying little tendency, as compared with the cats, to use this sense in finding the new situation of the box.

He reports also (960) that dogs cannot recognize photo-

graphs of objects. Buytendijk (150), on the other hand, finds that a dog can identify a triangle when its position and size are altered, and Orbelli (735) obtained evidence by Pawlow's method that dogs could appreciate both form and size differences.

The dancing mouse could not learn to distinguish two equal illuminated areas of different forms (1113). Raccoons learned to discriminate a round card from a square one (180). Thorndike taught the two Cebus monkeys under his observation to come down to the bottom of the cage for food when a card bearing the word "Yes" printed on it was exposed, and to stay up when one bearing the letter "N" was shown. The conditions seem to have been complicated, however, by the fact that the two cards were not placed in quite the same position. Further tests with cards carrying various designs showed varying degrees of capacity to distinguish them on the part of the monkeys (969). Kinnaman got negative results with his two *Macacus* monkeys in attempting to train them to distinguish cards such as those used in the later experiments of Porter on birds. His monkeys, however, proved able to distinguish vessels of different forms, "a wide-mouthed bottle, a small cylindrical glass, an elliptical tin box, a triangular paper box, a rectangular paper box, and a tall cylindrical can." These vessels differed in size as well as in form (540). Johnson's far more accurate experiments with the striped fields give the monkey a visual acuity about equal to that of man. Revesz (860) finds that monkeys are more influenced by form than by color in identifying stimulus objects; de Haan (66) finds the two factors about equally effective. In the experiments of Kohts (556) by her method of "choice by sample" (see p. 244 f.), the chimpanzee was able to distinguish solid as well as plane forms, and to recognize, although not easily, the likeness between an object and a drawing of it. When the drawing was two or three times larger or smaller than the object, the ape could still identify the two, although of course with a higher percentage of error.

The question has been raised as to just what is meant by the term "form" in connection with the visual perceptions of an animal. When Bingham (70, 71) found that a chick failed to recognize a triangle whose base instead of its apex was uppermost, he suggested that the chick's previous discrimination of the triangle from a circle was not a discrimination of form in the true sense of the word, but based "on the unequal stimulation of different parts of the retina." Hunter (481) thinks that the animal in such a case is really discriminating *pattern* rather than form, and by pattern he means the whole design presented by the lighted forms and their surroundings. That is, a square lighted area inside a round tunnel would present to the animal a different pattern from a square lighted area inside a square tunnel; an animal might fail to recognize that the forms of the squares were identical when they were presented as parts of such different patterns. The writer of this book suggested in a review of Bingham's work¹ that his chicks, in failing to recognize that a triangle with apex down is the same form as a triangle with apex up, were demonstrating not their deficiency in form vision, but their lack of an abstract idea of triangularity. This is a problem which will be discussed in Section 72.

Special evidence of the comparative development of the visual image in different genera of ants is suggested by Wasmann to be furnished by the facts of mimicry. Certain insects belonging to orders other than the Hymenoptera inhabit ants' nests, and have in many cases become more or less modified to resemble their hosts. Wasmann thinks that these resemblances, which have been established on account of their protective value, are in insects living among ants of well-developed visual powers, such as would deceive especially the sense of sight, while in the "guests" of ants whose vision is poor, the mimicry is adapted to produce tactile illusions (1041).

¹ Psych. Bull., vol. 10 (1913), p. 320.

End

§ 68. *The Homing of Animals as Evidence of Image Vision*

The ability to find their way back to their dwelling place, or to any other locality that has a vital significance for them, is a power widely distributed among the most various forms of animals. We have considered, in the chapter on the Chemical Sense, the part which smell plays in this process, and on page 89 we noted the fact that the perception of light direction is not wholly without influence in some cases. The common human method of path-finding is by the recognition of visual landmarks: when we set out from a familiar region into a strange region, we fix our attention on the appearance of the surroundings at critical points and turnings, and on the homeward journey guide ourselves by identifying these points through vision. Where it can be shown that animals are influenced in their homing journeys by the appearance of the surroundings, we have evidence that their vision must involve some perception of the form and detail of objects. The fiddler crab "remembers" the location of its nest, but just what the memory depends upon is not clear. On one occasion the observer, Pearse (780), covered the nest with his foot; the female crab to which it belonged waited fifteen minutes until he removed his foot, and then dashed for the nest and tried to reopen it. Lubbock's (610) demonstration that ants do not use visual landmarks on frequented roads will be recalled (see page 85).

In the case of bees, on the other hand, there is a good deal of evidence in favor of the use of visual landmarks in homing. It is true that Bethe (61) was unable to note any disturbance in the flight of bees back to the hive when he altered the appearance of the hive, or when a large tree that stood near the hive was cut down. But in this case the bees had thoroughly learned the location of the hive and had probably ceased to need landmarks in its immediate environs. Lubbock found that bees from a hive near the seashore, when taken out on the water and liberated, were unable to find

their way home, although the distance was less than their usual range of flight on land; and he ascribes their failure to the lack of visual landmarks to guide them (610). Bethe, who thinks bees are guided home neither by vision nor by smell, but by an unknown force to which they respond reflexly, also liberated some bees at sea about 1700-2000 meters from their hive, which was near the foot of Vesuvius and beside some very tall and conspicuous trees. The bees failed to return, and Bethe thinks, if they were guided by vision, the mountain and the trees should have aided them to do so (63). It may well be, of course, that bees cannot see objects at such a distance. Besides his observation that changing the appearance of a hive did not disturb the bees in their homing flight, Bethe urges against the visual memory hypothesis an observation on a hive which had on one side of it a garden, and on the other side a town, which he thinks the bees never visited, as food was to be had in abundance in the garden. Yet when liberated in the town they flew back to the hive with an accuracy certainly not born of their acquaintance with the locality (61). Von Buttel-Reepen, however, doubts whether the bees really never visited the town. Bethe's most striking illustration of his unknown force, however, is derived from his "box-experiments." If a number of bees are carried in a box some distance from the hive, on being liberated they fly straight up in the air. Some of them will return to the hive, but if the distance is great enough, many will drop back upon the box. Now if the box has moved only a few centimeters away during the flight of the bees, they will drop back to the precise spot where it was, and take no notice of its new location. If they were guided by vision, Bethe urges, they could easily see the box (61, 63). This, says von Buttel-Reepen, is arguing that their visual memory must be like ours if it exists at all; it may be a memory, not of the appearance of the box, but of its locality. He himself, repeating Bethe's experiments, observed the bees on dropping back after their upward flight, hunting

not at the place where the box had been, but at a height which was about that of their home hive entrance. He thinks that an important feature of the bee's visual memory consists in a power of accurately estimating height above the ground. If the entrance to the hive be raised or lowered 30 cm., all the returning bees will go to the old place, and it will be hours and sometimes days before they find the new one. Moreover, the same bees tend to return to the same corner of the opening each time. When a row of hives had been arranged, some with openings in front and others with openings at the side, bees which had been driven home in haste by a storm would sometimes try to enter the wrong hive, but if their home hive opened on the side, they would attempt to enter the foreign hive on the corresponding side (139).

Turner (988) reports that the burrowing bees (*Anthophoridæ*) use visual landmarks to identify the location of their nests, and are disturbed if the landmarks are altered.

In the solitary wasps, although Fabre is inclined to assume a "special faculty" of homing, independent of visual memory, basing his assumption on experiments where the wasps returned to their nests, from which they had been transported in a box to a distance of three kilometers (292, Series I); yet the evidence obtained by the Peckhams seems fairly conclusive in favor of memory for visual landmarks. The solitary wasps have been shown by the observations of the Peckhams to depend upon sight for the return to the nest (784, 785), and the same conclusion is indicated for the social wasps by Enteman (278). The Peckhams' belief in the visual memory of solitary wasps rests first upon the fact that the wasp, upon completing her nest, always spends some time in circling about the locality, in and out among the plants, as if she were making a careful study of the region. On leaving the nest a second time she omits this process and flies straight away. A similar "locality survey" is made by hive bees and by social wasps. Secondly, the Peckhams argue that if the wasp does not remember her nest by landmarks, it ought to make no

difference to her when the surroundings are altered in any way. They found, however, that a wasp of one species could not discover her nest when a leaf that covered it was broken off, but found it again without trouble when the leaf was replaced. Another wasp abandoned the nest she had made for herself with much labor, because the Peckhams, to identify the spot themselves, drew radiating lines from it in the dust. A third argument against the existence of a special sense of direction is the fact that wasps sometimes are unable to find their nests. In one case the Peckhams dug up the nest of a wasp and she made another five inches away. After an absence of three hours the wasp returned, and seemed to be puzzled as to whether the old spot or the new one were the place of her nest. "At first she alighted upon the first site and scratched away a little earth, and then explored several other places, working about for twelve minutes, when she at last found the right spot." Similarly, when a wasp that was carrying her prey left it for a few moments to go to the nest, as many of them do, apparently to see that all is right there, if any of the surrounding objects were altered she often had great difficulty in finding the prey again. On one occasion a wasp of another species dug its nest in the midst of a group of nests of the *Bembex* wasp. These latter are usually dug in a wide bare space of earth which has no vegetable growth to serve as a landmark. When the intruder had finished her nest, it looked just like the *Bembex* holes. She went away, secured a spider, and when she returned she could not find her nest. "She flew, she ran, she scurried here and there, but she had utterly lost track of it. She approached it several times, but there are no landmarks on the B. field. After five minutes our wasp flew back to look at her spider," which she had dropped about three feet away, "and then returned to her search. She now began to run into the B. holes, but soon came out again, even when not chased out by the proprietor. Suddenly it seemed to strike her that this was going to be a prolonged affair, and that her treasure was ex-

posed to danger, and hurrying back she dragged it into the grass at the edge of the field, where it was hidden. Again she resumed the hunt, flying wildly now all over the field, running into wrong holes and even kicking out earth as though she thought of appropriating them, but soon passing on. Once more she became anxious about the spider, and, carrying it up on to a plant, suspended it there. Now she seemed determined to take possession of every hole that she went into, digging quite persistently in each, but then giving it up. One in particular that was close by the spider seemed to attract her, and she worked at it so long that we thought she had adopted it, for it seemed to be unoccupied. At last, however, she made up her mind that all further search was hopeless, and that she had better begin *de novo*; and forty minutes from the time that we saw her first she started a new nest close to the spider, as though she would run no more risks" (784). An occurrence of this kind certainly lends color to the "recognition of landmarks" theory. On the other hand, the *Bembex* wasps themselves find their nests with unerring accuracy, though there is no landmark in the field. Fabre noted that *Bembex* wasps could not be led astray by any modification of either the look or the smell of their nests, and thought a peculiar form of space memory, unparalleled in our own experience, must be involved in the nest-finding of this species (292, Series I, 263). Bouvier, repeating Fabre's experiments on *Bembex*, obtained a different result. When a stone, for example, that had been at the mouth of a *Bembex* nest was moved a distance of 2 dm., the wasp, returning, went to the stone. Bouvier accordingly maintains the visual landmark hypothesis (115). Ferton holds the same view with regard to a species of wasp that makes its nest in shells. If during successive absences on the wasp's part the shell is moved from position A to position B, and later from B to C and from C to D, the wasp, returning, goes in turn to each of the positions that the shell has occupied. "In time, she omits to go to A, then to B. Little by little, the image of

the previous locations of her nest is effaced in the insect's memory." When she has found it, after each displacement, she makes a new "locality survey," before starting off again (293).

Turner (993) reports that the mason wasp is certainly guided by visual landmarks. A wasp had built her nest on a window casing. The window was one of four in a row; the shades on the other three were down. When the shade on the window where the wasp's nest was situated was drawn down and that of the next window drawn up, the wasp returning sought her nest on the casing of the next window, which was now the only light one in the row.

Solitary wasps and bees, which need to find their way back, not to a nest whose position remains fixed, as is the case with ants and honey bees, but to nests in new positions from day to day, almost certainly have to depend upon their recognition of visual landmarks, and hence we have another evidence that the compound eye can give a serviceable image.

The migration of birds is still an unsolved problem. That carrier pigeons depend on visual landmarks is maintained by many authorities. They do not fly at night, nor do they home well in cloudy weather. Young pigeons have to be trained on short distance flights, though of course this might be the case if they depended on some other power than recognition of visual landmarks. Migrating birds in some cases fly long distances over the ocean, where no visual clues can be furnished. Watson (1049) caused some noddy and sooty terns to be carried in a steamer from the Tortugas Islands to the latitude of Cape Hatteras, a distance of nearly a thousand miles, where they were liberated. The locality is far out of their range of habitat, yet they returned to their breeding place in about a week. Hachet-Souplet¹ suggests that a very vague visual image, of objects too far off to be clearly seen, may be used in such long distance homing, but the curvature

¹ VI Congrès Int. de Psychologie, 1909, p. 663. I have been unable to obtain the original article.

of the earth would interfere with a bird's getting even a vague image of any surroundings that could be familiar to it.

§ 69. *Class V: Reactions adapted to the Distance of Objects*

The factors that make possible the perception of the third dimension, depth, or distance outward from the body, in invertebrate animals are little known. Certain invertebrates do give evidence of the power to judge distance. The hunting spiders, for example, which do not make webs, but pursue their prey in the open, leap on it from a distance of several inches. Dahl thinks their distinct vision is limited to two centimeters (226), and Plateau says capture is not attempted until the prey is within this distance (812). The Peckhams, however, tested a hunting spider by putting it at one end of a narrow glass case sixteen inches long, at the other end of which a grasshopper was placed. When eight inches from its victim, the spider's movements changed, and at four inches the leap was made.¹ (783).

Baldus (22) has made an interesting study of distance perception in the aquatic larva of a dragon-fly. When prey, which must be in motion, is dropped into the water, the larva fixates it binocularly, that is, turns the head straight toward it; approaches, but does not snap until the food is within reach of the lip. Now two-thirds of those facets of the larva's compound eyes which can be simultaneously and equally stimulated are affected only by objects within the lip's reach. Hence the snapping reaction probably occurs when a sufficient number of these are excited by the object. If one eye is removed, the snapping is much less accurately adjusted to distance. A one-eyed larva, however, can adjust to distance on the basis of the size of the image: about sixty facets of the eye must be stimulated to produce the snapping reaction.

¹Porter (830) observed that the distance at which spiders of the genera *Argiope* and *Epeira* could apparently see objects was increased six or eight times if the spider was previously disturbed by shaking her web. This, of course, does not refer to the power to *judge* distance.

Reactions of this character, where the animal makes a single movement adapted to the distance of an object from it, are almost the sole evidence we can get of accurate perception of the third dimension. The alleged performance of the jaculator fish, which, as described by Romanes, "shoots its prey by means of a drop of water projected from the mouth with considerable force and unerring aim," the prey being "some small object, such as a fly, at rest above the surface of the water, so that when suddenly hit it falls into the water," would involve distance perception (872, p. 248). The catching of insects on the wing by various amphibians, reptiles, and birds has the same significance. A salamander cautiously stalking a small fly will not strike until it gets within a certain distance. In *Necturus* and in other animals the pause just before snapping at food has been suggested to be for the purpose of proper fixation (1071).

Training an animal to jump from one support to another is a method that has been used to study distance perception in the mouse (1056) and white rat (863). Waugh put a mouse on a disk and raised it a certain distance above a support; he then measured the time the mouse hesitated before jumping, when the height of the disk was varied. From the fact that the mice hesitated longer, the greater the height, he inferred some visual perception of distance. When, however, the mice were required to judge which of two partitions was nearer to their starting-point, and to turn to the right or the left in accordance with this preliminary judgment in returning to their nest, they failed: this really involves a rather complex type of learning, and is a much less fair test of the mere ability to perceive distance than is the instinctive reaction of jumping. In Richardson's (863) study of the rat, the animals were trained to jump from one horizontal support to another. They proved able to judge quite accurately the direction of the platform to which they had to jump, but when its distance was altered they could not adapt themselves, and jumped either too far or too short.

Yerkes's tests of the so-called "sense of support" in tortoises indicate, like Waugh's experiments on the mouse, some power of estimating distance by vision in these animals. He experimented, it will be remembered, with individuals belonging to three classes: land-dwelling, water-dwelling, and amphibious. The first mentioned would crawl off the edge of a board 30 centimeters above a net of black cloth only with much reluctance when their eyes were uncovered; when blindfolded they would not move at all. The water tortoises plunged off without hesitation from a height of 30 centimeters, but hesitated slightly at 90 centimeters, although some individuals would take the plunge at once even from a height of 180 centimeters. When blindfolded, all of the water tortoises rushed off at any height. The land-and-water-dwelling tortoises hesitated at 30 centimeters and at 90 centimeters showed a conflict of impulses, trying to catch themselves before launching off. When blindfolded they would not leave the board at all, though they moved about upon it freely (1103).

Some of the most important conditions of distance perception in our own experience are lacking in the lower vertebrates and in invertebrates. Stereoscopic vision, the appearance of solidity given to objects by the fact that the visual fields of the two eyes combine, thus producing blending of two slightly different views of the object looked at, has been held to be dependent on the partial crossing of the optic nerves on their way to the brain, whereby each retina sends nerve fibres to both hemispheres of the brain. This arrangement does not appear in the animal kingdom below the birds; whatever function it plays in space perception is, then, absent from reptiles, amphibians, fish, and invertebrates. Certainly stereoscopic vision cannot exist in animals whose eyes are so placed that the same object cannot be seen by both, as is the case with most fishes. Hess (432), by the way, has shown that the monocular visual field in fish is much more extensive than in man. Fish can see objects directly above them. In birds whose eyes are situated too far toward the sides of the

head for the same object to cast its images on the foveas or centres of the two retinas, there appears to be a secondary fovea in each eye, so placed as to suggest that it serves binocular vision, while the primary fovea is used for monocular vision. In certain mammals the eyes are placed so far towards the sides of the head that the binocular field is very small. This is probably the reason why rodents do not have a more accurate perception of distance. The writer made some simple tests on the use of binocular and monocular vision by the rabbit (1035). When the animal was sitting quietly, two bits of food of equal size and kind were held at equal distances from the rabbit's nose, one straight in front, the other directly to the right or left of the rabbit's head. In forty-eight out of fifty trials, the rabbit turned towards and secured the food at the side rather than that in front, thus showing its dependence on monocular rather than binocular vision.

Convergence, the turning of the eyes toward each other to bring the two images of an object on the central part of the retinas, which is an important aid to human estimation of distance, is also necessarily lacking in animals without binocular vision. A third factor in our own perceptions of distance, the accommodation of the crystalline lens, that is, the alteration of its convexity through the pull of the accommodation muscle to enable it to focus objects at different distances, has been carefully studied in connection with the lower animals by Beer. Through experiments on the refractive powers of eyes dissected from the dead animal, he reached the conclusion that no invertebrates but cephalopods have the power of accommodation. It is rudimentary or lacking also in some members of the fish, lizard, crocodile, snake, and mammal families. In cephalopods, fishes, amphibians, and most reptiles, the process of accommodation does not involve a change in the form of the lens, but an alteration in the distance between the lens and the retina. The device of increasing the curvature of the lens for vision of near

objects appears first in certain snakes, and is found throughout the higher vertebrates (42, 43, 44, 46).

Where accommodation does not exist, as in most invertebrates, it is possible to trace other arrangements for adapting vision to the distance of the object seen. Thus in compound eyes, part of the eye may be adapted to near vision and part to far vision. This is suggested by the fact that some of the little tubes, or ommatidea, of which the compound eye is composed, diverge from each other by a less angle than others, indicating that they are suited to the reception of more nearly parallel rays. In insects with both simple and compound eyes one form may be used for near and one for far vision. It has been maintained (247) that the simple eyes function with the compound eyes to respond to changes in the depth of objects, since such changes would alter the angle at which light rays from the object would fall on the two sets of eyes. Spiders appear to have the principal eyes adapted for far vision and the auxiliary eyes for near vision, while one spider, *Epeira*, has part of the hinder median eye adapted to each (448).

§ 70. *Tactual Space Perception*

There is little experimental or observational material on the tactual perception of space by animals. Darwin (229) made observations on earthworms which line their burrows with leaves, leading him to conclude that they perceive by touch the shape of the leaves, which they draw in by grasping them near the apex. Darwin and Hanel (385) attempted to meet the obvious suggestion that the leaves may be drawn in point first because they resist being drawn in any other way, by scattering paper triangles about the burrows. When these had been pulled in, they were dug up, and the absence of creases was taken as evidence that there had been no attempt to pull them by the basal edges. Neither Darwin nor Hanel actually observed the worms at work. Jordan (522) and Mangold (634) did, and report that there is no ex-

ploration of the form of the leaves: they are seized at any point, but only those seized near the apex get into the burrow. Kafka (523) suggested that the parts further from the stem may offer a different chemical stimulus to the worms from that presented by the stem, and Mangold (634) proved this experimentally.

Goldsmith (357) has described the behavior of a hermit crab while hunting for a new snail-shell to occupy. The eyes are not used at all in this process. She offered the crab wax figures of various forms, cones, pyramids, spheres, cubes, cylinders. The crab examined them impartially, showing no especial interest in those most resembling the form of a snail-shell. The case was different where size was concerned. Of two spheres of different sizes, the one best corresponding to the size of the crab was explored on an average 23 seconds; the smaller one only 10 seconds. Of two cones equal in height but differing in their bases, the one corresponding to the animal's size was explored much longer. Probably it was merely easier to "handle."

§ 71. *Some Theoretical Considerations*

The temptation is strong to speculate upon the essential nature of the conditions which make possible true space perception, the simultaneous experiencing of sensations that are referred to different points in space. Such speculation must be of the most tentative description, yet the following suggestions seem not wholly unwarranted by the facts. For one thing, it looks probable that the ability to suspend immediate reaction is essential to space perception. Can a spatial complex of sensations occur in the experience of an organism unless that organism is capable of receiving a number of stimuli on a sensitive surface and of suspending, for a brief period at least, all reaction? Let us take as an example of such a complex a visual field, within which different color and brightness qualities are arranged in definite order, some above,

some below, some to the right, others to the left. Could such a balance of tendencies to move the eye as is involved in the simultaneous perception of a number of elements preserving regular space relations to each other have been brought about unless no single one of the tendencies were irresistible? One can readily imagine an eye functioning in such a way that every stimulation of it, though occasioned by rays from several different directions acting simultaneously, should issue at once in a resultant movement. Would not the accompanying consciousness be a single resultant sensation, rather than a complex of spatially ordered elements? It is a good deal easier, of course, to ask than to answer such questions.

Again, the power of getting true spatial images seems to be bound up closely with the power of moving the sensitive surface. We get our best tactile space perceptions through active touch, involving movements of the hands and fingers; our visual perceptions are profoundly influenced by eye movements. Where the movements of an animal's body as a whole are very rapid, as in the case of winged insects, this fact may compensate for the immovability of its eye. Forel, as we have seen, thinks that insects which can explore objects by moving the antennæ, bearing the organs of smell, over them, may have smell space perceptions, such as are unknown to our experience; they may perceive the shape and size of odorous patches as we could do if our organs of smell were on our hands (310). Now, movement of a sense organ brings about the same result that movement of a stimulus across a resting sense organ does; that is, the stimulus affects different points of the sensitive surface in succession. But the vital significance of the two is quite different; movement of an object across a resting sense organ means very likely that the object is alive; it must be instantly reacted to, and the speed of the reaction is unfavorable to the formation of a true space perception. Movement of the sense organ, however, gives a series of impressions on successive points of the sensitive surface, from a resting object. While the sense organ

is being moved, it is probable that other reactions of the animal will be suspended. Whether any part in the formation of that complex conscious content which we call a spatial image, consisting of different sensations simultaneously apprehended, is played by the "lasting over" of the impressions on one sensitive point after the stimulus has passed on to the next, a phenomenon which we find both in touch and in sight sensations, it is impossible to say. We are, however, apparently justified in the statements that the essence of space perception, as distinct from other conscious processes that may accompany spatially determined reactions, is the presence of an image in the sense above defined, and that a movable sense organ is an important condition for the production of such an image.

§ 72. *The Perception of Things*

In Chapter IV we said that the conscious analysis of its environment by an animal depends on the structure of the animal's sense-organs and upon its abilities to move. In the chapters which followed we discussed the ability of animals to analyze out of their environment different sensory qualities, such as colors, tones, and smell qualities. Now ordinarily, when anything is analyzed, it is broken up first into large pieces and later into small ones. Thus one might argue that the analysis of one's environment into those larger fragments called things would precede the discrimination of those minuter elements called sensory qualities. But when we survey the facts of animal discrimination we see that this is clearly not the case, so far as the development of discriminations up through the ascending series of animal forms is concerned. For example, the visual discrimination of things certainly demands as its basis a visual image, but animals of so low an organization that their eyes cannot give visual images are quite capable of discriminating different visual qualities. These qualities must be perceived against some kind of con-

scious background, but the background is not a visual field filled with objects.

A school of German psychologists, sometimes called that of the configurationists, has been recently emphasizing the great importance of the background against which, or out of which, discriminations are made. For the lower animals this has been done especially by Volkelt (1021). He takes the extreme view that in their case analysis from the background is always highly incomplete. Only on this supposition, he thinks, can we explain the occasional failures in the execution of instinctive acts. He had, for example, under observation a web-making spider, which, when a fly was caught in the web, displayed all the usual skill in despatching it; but when a fly was placed in the little nest where the spider lurked, beside the web, the spider actually fled from it. This shows, argues Volkelt, that the total situation is the determining factor in the spider's behavior. To the spider a fly in the web is not the same *thing* as a fly out of the web; in fact the world of the spider is not made up of things at all. This conclusion, he holds, is supported by such observations as Bethe's that a bee hesitates to enter the hive if it has been moved, or the Peckhams' that a solitary wasp will not recognize her nest if its surroundings are altered. "If the total situation created by the part-event is not provided for as the stimulus for any specific reaction, the animal must in regard to the part-event, indeed to the total situation, be wholly inadequate." The same general conclusion is reached by Buytendijk, studying the effect of altered general environment on a dog's ability to select a particular compartment in a multiple choice apparatus (see page 301). Such changes as rotation of the apparatus, removing a white disk over the door, and cutting off two of the other compartments, produced disturbances in certain individuals; sometimes the removal of a landmark was felt as a disturbance only after several trials. Instances of the influence of general environment on maze running will be found on pages 283 ff.; but

it should be noted that the point concerned here is not that certain features in the environment may be used as landmarks to determine reaction, that is, may be *the* stimuli reacted to; but that the whole environment coöperates in determining the response.

Against the extreme position of Volkelt, that animals do not live in a world of things, objections are urged by Demoll (246) and Bierens de Haan (64, 65, 66). The former argues against Volkelt's interpretation of the spider's behavior, that such activities as the capture and killing of flies are chain-reflexes; each step in the process will occur only if preceded by a certain other step. (We should call them congenital movement systems, part of the stimulus for a given movement being furnished by kinesthetic excitations from the performance of its predecessor). Hence the spider will not go through the movements of attacking and securing a fly unless it has previously performed those of running out to the fly along a radius of its net. De Haan thinks the spider's failure to seize the fly is due to general (emotional?) disturbance, and that it does not prove that the spider fails to recognize the fly as a distinct thing: if a man is in the habit of gazing quietly at a tiger in a cage and one day encounters the tiger at liberty, does his altered behavior prove that he does not recognize the tiger as a thing because "tiger-in-cage" and "tiger-loose" determine such different reactions on his part?

Clearly, the facts indicate, not indeed that there are no things in the world of an animal's consciousness, but that an animal and a man would in the same environment perceive different portions of the environment as things. A dog shut up in a box with food on the outside shows no tendency to react to a latch at the door; a man in an analogous situation would react to it at once (See pp. 271 f.). The latch is not a thing to the dog; it is to the man. We have met in various experiments on the discrimination of sensory qualities and on space perception, and we shall meet in experiments on

learning, instances where the animal proves to be reacting to features of the environment quite other than those to which the experiment is directed; the experimenter perceives one set of things in the situation, the animal a different set.

It is the manner in which a man or an animal moves with relation to the features of his environment that chiefly determines the formation of "things" in his consciousness. Evidence for this assertion will appear if we try to put ourselves into the position of a creature that has no power to move things about. Suppose that we had no grasping organs; no means of picking up things and moving them from one position to another. All the inanimate parts of our surroundings would be reduced to the status of mere landscape, even though our eyes could give us clear images of them. Living creatures, moving themselves independently of their background, would be things because we could react to them independently. If you are asked to enumerate the things in a room, you are likely to enumerate the parts of your environment that you can move independently of one another. Thus we can understand why elephants, with a free grasping organ in the form of a trunk; raccoons, in the habit of sitting on their hind-legs and using their paws to handle objects, and monkeys learn so readily to behave towards their environment in a more or less human fashion.

The problem as to how an animal analyzes its environment underlies all experiments on animal behavior. There are certain experiments, however, which bear more especially upon it. One class of such investigations comprises the cases where an animal apparently reacts, not to either of two stimuli, but to the relation between them. In the writer's (1035) study of color vision in the rabbit occurred an instance of this kind. The rabbit had been trained to push at a red door rather than a grey door, the places of the doors being of course exchanged from time to time. She was choosing the grey only 24% of the time. These experiments were then intermingled with others where the same grey appeared on one

door and white on the other. Previous work had shown that the rabbit saw red as a very dark grey. In the grey-white tests the grey was chosen 73% of the time. In such cases it looks as though the stimulus were "darkening," rather than an absolute grey value. Similar results in brightness discriminations were obtained by W. Köhler on fowls and monkeys (549, 552), and by the Amsterdam laboratory on guinea-pigs (1080). Riekell (866) found that the habit of reacting to the brighter of two simultaneously presented greys could be carried over by fowls into tests where the greys were shown successively. His fowls succeeded in thus comparing the size of figures. Bingham's (72) chicks, trained to react to a larger rather than a smaller area, showed no disturbance when the absolute sizes were altered, although they were thus required to choose the very area that had been the "shock-stimulus" in the preceding experiments.

Two interpretations may be put on such behavior, the one being that it indicates *recognition of the relation* "larger than" or "brighter than" for its own sake, the other that it means *failure* on the animal's part to *recognize any difference* in the two total situations. Lloyd Morgan's canon would incline us to the latter interpretation. In the case of brightness differences, the power of brightness adaptation in the eye would account for inability to recognize absolute brightnesses: we ourselves are surprised to learn that snow in moonlight is many times darker than black velvet in ordinary daylight. Possibly the relation "larger than" may be reacted to as such, but the character of triangularity could not be, the reader will recall, by Bingham's chicks (see p. 224), nor by monkeys in the experiments of Revesz (861). Although after training with forms cut out of colored papers, they could recognize the same figures drawn on white paper, they failed, when trained to choose an equilateral triangle, to transfer their response from this figure to triangles with acute or obtuse angles at the apexes. Again, the attempt was made to see whether monkeys could be trained to recognize *doubleness*.

Five figures were used: a smaller circle, a larger circle, a vertical ellipse, a horizontal ellipse, and two small circles side by side. The last was the figure to be chosen. The monkeys learned to choose it, and continued to react to it even when the circles were placed one over the other instead of side by side. They failed, however, when the circles were made much larger, and when squares were used instead of circles. It was not doubleness to which they were reacting, but doubleness in a certain setting (65).

All such observations show the influence of the total situation upon discrimination. A similar influence, it is claimed by de Haan (66), appears in the following observation: monkeys were trained to react to a red cross rather than to a blue triangle; they were then offered the choice between a red cross and a blue cross, and failed to discriminate, indicating that the color had not been influential in the previous discriminations. But when offered a red cross and a red triangle, they failed again: evidently, the experimenter concludes, they had learned to react to a red cross only in the blue triangle situation.

This work of de Haan's is an instance of a second type of investigations, whose aim is to show which of two aspects of a situation is more readily analyzed out of it. For example, Revesz (860), using the Multiple Choice Method, after some tests on the monkey's ability to distinguish among forms of different color and colors of different form, trained it to choose a figure differing both in form and in color from the other three figures presented. He then offered the animal a choice of four figures, among which were one like the training figure in form and one like it in color. The monkeys sometimes chose one, sometimes the other, but on the whole form determined the greater number of choices. When trained to choose a green triangle among four differently colored triangles, and then shown four figures, one a green circle, the others differing both in form and color from the training figure, the monkeys chose the green circle, indicating that the color had been

"noticed"; but when offered an orange circle, a green pentagon, a yellow square, and a blue oblong, they chose the circle, form here dominating color. And when shown eight differently colored circles they reached for all indiscriminately. De Haan (66) does not find this dominance of form. In an investigation (65) on the monkey's ability to compare the length of lines, it developed that the animal was really reacting to a wholly different clue. He could see through the cracks of the compartment doors which door was not bolted, and when they were all left unbolted, his discrimination broke down. In later series he proved to be influenced by features of the cards which could not be detected by human vision, for when new cards, to the experimenter's eye exactly like the old ones, were used, the percentage of error rose, for easy discriminations, from zero to 28, and for hard discriminations from zero to 55. Yet when cards were prepared which had actual slight differences, spots or unevennesses, this perverse monkey could not learn to distinguish them from each other. De Haan's conclusion is that the monkey does not perceive what we perceive; that his visual image is less analyzed, and that the elements dominating in it are other than those which would dominate in our own case. The vital importance of different elements to the animal is influential here: that so small a detail as the open crack beside the unbolted door should be fixed upon by the monkey may be explained, it is suggested, by the general interest of the monkey kind in cracks, which they like to explore for insects.

The most elaborate experiments yet made on the process of abstraction, as the analysis we are discussing is often called, are those of Kohts (556) on a chimpanzee. Her method itself involved a difficult problem in perception: it was to hold before the animal a sample object and require him to choose among a number of objects one like the sample. The stimuli comprised a great variety of pigment colors and greys, and forms both plane and solid. As may be imagined, it took much time, patience, and ingenuity to make the ape realize

what he was expected to do. He perfectly mastered the method, however, under conditions which seem to have excluded the influence of clues unintentionally given by the experimenter. When he had learned to choose an object resembling the sample in all respects, he was trained to select one like it in some one respect only. This he did most successfully in the case of color, learning to put in a box of a certain color all the objects of that color before him. But this achievement was obviously much harder for him than the choice of wholly similar objects. It is noteworthy that he showed no evidence of learning when the attempt was made to get him to associate an object with the sound of its name.

CHAPTER X

THE MODIFICATION OF CONSCIOUS PROCESSES BY INDIVIDUAL EXPERIENCE

THE reactions of animals to stimulation show, as we review the various animal forms from the lowest to the highest, increasing adaptation to the qualitative differences and to the spatial characteristics of the stimuli acting upon them. It is therefore possible to suppose that the animal mind shows increasing variety in its sensation contents, and increasing complexity in its spatial perceptions. But besides this advance in the methods of responding to present stimulation, the higher animals show in a growing degree the influence of past stimulation. While a low animal may apparently react to each stimulus as if no other had affected it in the past, one somewhat higher may have its reaction modified by the stimulation which it has just received. An animal still more highly developed may give evidence of being affected by stimuli whose action occurred some time before; and finally, in certain of the vertebrates, perhaps, as in man, conduct may be determined by the presence in consciousness of a memory idea representing a past stimulus. "Learning by experience," or "associative memory," as we saw in Chapter II, has been regarded as the evidence *par excellence* of the existence of mind in an animal. That it does not serve this purpose to entire satisfaction was also pointed out in that earlier chapter, and will be more clearly apparent as we survey in the following pages the various ways in which an organism's past experience may modify its behavior. For each type of modification we shall try to find a parallel in human experience, and thus to interpret, so far as possible, the conscious aspect of the

learning process. To begin with, we shall distinguish between those modifications which depend on some comparatively lasting alteration in the organism (in its nervous system if it has one), that is, the kind of modification which is ordinarily understood by the term "learning"; and modifications which are due to a change essentially temporary in its character, in the physiological state of the organism. Even in the lowest animals the effect of a stimulus depends on the organism's physiological condition, and this condition is often the result of stimulation recently received.

§ 73. *Modifications Due to Essentially Temporary Physiological States: (a) Heightened Reaction as the Result of Previous Stimulation*

Sometimes the effect of the stimuli which the organism has just received increases the violence of its response to a given stimulus. Shelford, studying the effects of a wide variety of stimuli in various intensities upon animals ranging from protozoa to mammals, states as a general law that an animal becomes more sensitive to a stimulus after encountering a high intensity of it; and asks whether this may not be true learning, the weak stimulus being taken as a warning of high intensity to come (917). This is a question which could be answered by suitable experiments. In the earthworm Jennings points out that various stages of excitability may exist, due to the action of previous stimulation, and varying all the way from a state of rest, where a slight stimulus produces no effect, to a condition of violent excitement, where moderate stimulation will cause the animal to "whip around" into a reversed position or wave its head frantically in the air (511). This increased excitability suggests the "nervous irritation" produced in a human being by an accumulation of disagreeable stimuli; an increased feeling of unpleasantness accompanied by more diffused organic and kinæsthetic sensations is its accompaniment in the human mind.

When the same stimulus is repeated, in many cases the effect of this heightened excitability is shown by the organism's performing in succession different forms of the negative reaction until one of them is successful in getting rid of the stimulus. The ciliate *Stentor* furnishes us with an example. When attached by its stem, if it is strongly stimulated, say, with a glass rod, several times in succession, it first tries its commonest negative reaction, bending over to one side. If the stimulus continues, it reverses momentarily the direction in which the cilia are whirling. If this, several times repeated, does not succeed in getting rid of the stimulus, the animal contracts strongly upon its stem. This also is continued for some time, but if the stimulus too is kept up, the *Stentor* finally breaks from its moorings and swims off (504).

There are many examples of similar behavior in other animals. *Hydra* in certain cases tries first the ordinary negative response of contraction, and later moves away from the region it has been occupying (1024). Frandsen found that if the slug *Limax maximus* has a tentacle touched several times in succession, it at first withdraws the tentacle and turns away from the stimulus. Later, it may move toward and push against the stimulus, and do the same if the touch is on the side of its body, resisting and curving around the obstacle—another way, of course, of getting rid of it (314). Preyer, again, observed a very pretty instance of this sort of behavior in the starfish. He slipped a piece of rubber tubing over the middle part of one of the arms of a starfish belonging to a species in which those members are very slender, and found that the animal tried successively various devices to get rid of the foreign body, to wit, the following: rubbing it off against the ground, shaking it off by holding the arm aloft and waving it pendulum-wise in the air, holding the tube against the ground with a neighboring arm and pulling the afflicted arm out, pressing other arms against the tube and pushing it off, and, finally, as a last resort, amputating the arm. This, says Preyer, is intelligence, for the emergency

is not one normal to the animal, and it is adapting itself to new conditions (835). It would, however, be demanding too much even from intelligence to suppose that the starfish's behavior is entirely new. A human being, capable of ideas, could only, in a similar predicament, "think of," that is, call up, ideas of the behavior which on former occasions somewhat resembling the present had proved effective. Do such cases of the trial of different devices indicate that the animal concerned calls up any kind of idea or image of each device before putting it into practice? Decided evidence in favor of such a supposition might be furnished if the "trial and error" needed to be gone through with only once. A human being brought into such conditions and guiding his conduct by ideas would, if placed in a similar emergency soon afterwards, immediately recall the idea of the successful action and waste no time over the unsuccessful ones. But we have no reason to think that such is the fact with our primitive animals. Preyer's starfish, when confined by large flat-headed pins driven into the board on which it lay, close up in the angles between its arms, managed to escape by trying a large variety of movements, and gradually diminished, Preyer says, the number of useless movements made in successive experiments (835). O. C. Glaser, on the other hand, found that the echinoderm *Ophiura brevispina* does not improve at all with practice in removing obstructions from its arms. The very versatility of the starfish, this writer thinks, tells against its perfecting any one movement through experience (353). Stentor and Hydra go through the same series of reactions each time, without apparently being influenced by their previous behavior. And again we must remind ourselves that there is no reason why their conduct, adaptively regarded, should be otherwise. An animal with so little power of distinguishing qualitative differences among stimuli cannot be in any way aware that the stimulus which affects it a second time is going, as in the previous case, to be so persistent that the ordinary negative reaction will not get rid of it. Further,

each reaction of the series performed by the animal is more disturbing to its ordinary course of life than the preceding one. The Stentor can bend to one side and still continue the food-taking process; if it reverses its ciliary action, feeding must be momentarily interrupted; while contraction on the stem and breaking loose from its moorings are still more serious infractions of the normal routine. It would be decidedly disadvantageous to take the last step while there was any chance that milder measures might prevail.

In all probability, since the behavior just described has no permanent effect upon the animal, it is physiologically due, as Jennings suggests (509), to the overflow of the nervous energy set free by the stimulus into first one channel and then another. In most cases the movements resulting are all adapted to getting rid of the stimulus, though only one of them is successful in so doing; but we have on record one case where, in a supreme emergency, the stimulus being not only repeated but increased in intensity, every possible outlet is tried, whether it has any fitness to the situation or not. This was observed by Mast, testing the effect of increased temperature on the reactions of planarians. The first influence of such increase from 23 degrees to 26 degrees C. is to produce heightened activity and positive reactions. Then, from 26 degrees to 38 degrees, the reactions are negative. From 38 degrees to 39 degrees, violent crawling movements set in, and then, curiously enough, the righting reaction is given, perfectly irrelevant, of course, to the conditions. Finally, the anterior and posterior ends are turned under, the central part is arched upward, and the animal falls over forward on its back (642).

In all those cases where repetition of the same stimulus produces successively different forms of the negative reaction increasing in violence, it is most natural to think of the psychic accompaniment as an increasing degree of unpleasantness. In our own experience, repeating a stimulus does not alter the quality of the resulting sensation, except where

the structure of a special sense organ is a modifying factor, as in the case of visual after-images. A decidedly disagreeable stimulus acting repeatedly on a human being may produce unpleasantness that grows more and more intense until it is unbearable; the behavior of a human being under such circumstances is much like the animal behavior we have just been describing. Various movements calculated to get rid of the stimulus are tried, each more energetic than the last. Hence, if the lower animals behaving thus are conscious, we may plausibly assert that their consciousness under these circumstances is increasingly unpleasant. But the human experience in such a case would be, or might be, further characterized by the presence of ideas. That is, the human being would *think* of the different ways to get rid of the stimulus one after another. This many, at least, of the animals that try different negative reactions are apparently incapable of doing. We judge that they are so by the simple fact that on being subjected after an interval to the same presumably disagreeable stimulus, they do not at once make the reaction that was previously successful in getting rid of it. A human being, recalling that reaction in idea, would be able to do so. We shall see in the next chapter that many animals, while they do not learn the successful reaction from a single experience, do gradually diminish the number of unsuccessful ones made in a series of experiences. It is quite possible that this will prove to be true of all animals, as experimental evidence accumulates.

§ 74. *Modification Due to Essentially Temporary Physiological States: (b) Cessation of Reaction to a Repeated Slight Stimulus.*

The type of modified response just described occurs when the stimulus is strong, and presumably injurious. When it is of moderate intensity only, the organism tends to respond less and less violently as the stimulus is repeated at short inter-

vals, until finally the response lapses entirely. The Ciliata *Vorticella* and *Stentor*, which spend a part of their time attached to solids by a contractile stem, contract at the first application of a moderately intense mechanical stimulus, but fail to react at all when the stimulus is several times repeated (504). *Hydra* responds to mechanical stimulation by contraction, but gets used to the process when repeated and gives no further reaction (1024). The sea-anemone *Aiptasia* reacts by a sharp contraction to a drop of water falling on it; later it ceases its response to this stimulus. If exposed to light, it contracts and remains in this state for some hours, but afterwards expands again (508). The annelid *Bispira voluticornis* was found by Hesse to give no further response to sudden shadows when the stimulus was frequently repeated (445). Hargitt (386) reports the same of tube-dwelling annelids. Von Uexküll reports that the sea-urchin, *Centrostephanus longispinus* ceased to respond to shadows after three successive stimulations (1001). Nagel observed that certain eyeless mollusks which react to sudden darkening very quickly get used to the stimulus and cease to respond; often after one reaction they decline to react for several hours.¹ The mollusks that responded to sudden brightening rather than to shadows, that were in Nagel's phrase photoptic rather than skioptic, took longer to become accustomed to repeated stimulation, but did so by gradually weakening their reaction (720). A web-making spider that was found by the Peckhams to drop from its web at the sound of a large tuning fork declined to disturb itself after the stimulus had been repeated from five to seven times (782). Ants "become used" to the ultra-violet rays which they ordinarily avoid (296). The responses of

¹The opposite phenomenon is reported by Rawitz of the mollusk *Pecten*, whose response to a shadow was the shutting of its shell. Repeated or long-continued shadowing, instead of doing away with the reaction, caused the animal to remain with closed shell for a long time; an intensification of the reaction which suggests the effect of summation of stimuli (848). We may infer that the stimulus in such a case is injurious.

dragon fly nymphs to light are less marked as the stimulus is repeated (868), and the same is true of mosquito larvæ (464).

Where such an effect as this is temporary, the most obviously suggested cause for it is *fatigue*. In our own experience this word is used chiefly with reference to motor processes; we perceive a certain signal, but are too fatigued to respond. On the sensory side, when a repeated or continued stimulus is no longer perceived, we call the phenomenon one of *adaptation*. In true sensory adaptation, the sense organ becomes incapable of responding to the stimulus; for example, a person who has been for some time subjected to a certain odor is unable to smell it any more, however much he tries. Closely related to this phenomenon and yet different from it, is the lapse of attention to a repeated stimulus: we no longer notice the ticking of a clock, although the sense organ is unaffected by its continuance, and we can quite well hear it if our attention is attracted in that direction.

That the failure of Stentor to respond to successive stimuli is not due to motor fatigue appears quite certain to Jennings, since under favorable conditions he has obtained reactions from the animal for a period far longer than that occupied by the process of getting used to slight mechanical stimulation (504). And in most of the cases cited, the acclimatizing process seems to occur too rapidly to make fatigue of the motor apparatus probable. In the lower animal forms, sensory adaptation offers the most natural explanation for the phenomenon; in the higher animals, lapse of attention is very likely also involved. The modification of consciousness in both cases would be the loss of the sensation; where adaptation occurs, the sensation would be for the time irrecoverably lost; where there is merely lapse of attention, it could be regained by a proper direction of attention.

A much discussed case of the cessation of response to a repeated stimulus is found in connection with the food-taking reaction. One would expect the dominant condition here to

be loss of hunger, and as a matter of fact, observers of the feeding processes in many lower animals have found that such reactions cease or turn into negative responses when the animal is satiated; although Piéron indeed reports that while the responses of *Actinia equina* and *A. rubra* to mechanical stimulation cease on repetition of the stimulus, those to food stimulation continue indefinitely (796). If the change from food-taking to negative reaction has a conscious accompaniment, this might naturally be thought of as a change from pleasant to unpleasant affective tone. Nagel observed that if a ball of filter paper soaked in fish juice were placed upon one of the tentacles of the sea-anemone *Adamsia*, it was seized as eagerly as a ball of fish meat, but that when this deception had been several times repeated, the ball was held for a shorter period each time, and was finally rejected as soon as offered. Nagel is inclined to think that this is learning by experience, and points out that the psychic life of *Adamsia* must possess little unity, for the "experience" of one tentacle does not lead other tentacles to reject the paper balls at once (721). Parker finds similar behavior in *Metridium*, and explains it by saying that the filter paper offers but a weak food stimulus, and that "the successive application of a very weak stimulus is accompanied by . . . a gradual decline in the effects, till finally the response fails entirely"; in other words, that we have adaptation to a food stimulus (739). Jennings fed *Aiptasia* alternately with pieces of crab meat and with filter paper soaked in meat juice, the result being that the fifth piece of filter paper was rejected—but so was the crab meat thereafter. Jennings came to the conclusion that the phenomenon is due simply to loss of hunger on the animal's part, and that where Parker found that the crab meat would be taken after the filter paper was refused, it was because the latter was a weaker stimulus and naturally was the first to call forth the effects of satiety. The objection to the hunger hypothesis is that other tentacles of the same animal will react after one tentacle has stopped; satiety ought surely to affect the entire organism (508). Alla-

bach, in the light of these researches, made a careful study of *Metridium*. She disposes of the psychic learning by experience theory of Nagel by saying that the only experience upon which the animal could reject the filter paper must be experience that it is not good for food. This could be learned only by swallowing it; but the failure of the reaction occurs just as well when the animal is prevented from swallowing the filter paper. That the phenomenon is not one of adaptation to weak stimuli is shown by the fact that it may be brought about by successive feedings with meat which is not allowed to be swallowed. It cannot be due to loss of hunger, for this is experimentally shown to affect all the tentacles at once. Allabach concludes that it is simply a case of local fatigue of the tentacles. The taking of food by a tentacle involves the production of a considerable quantity of mucus, the immediate supply of which is probably exhausted after a few reactions, and a short period of rest is required(4). Parker (757) is still of the opinion that adaptation is the proper explanation for the phenomenon.

Another case of the cessation of reaction to a repeated stimulus is reported by Wasmann of ants in an artificial nest, which assumed the fighting attitude in response to the movement of a finger outside the nest, but after two or three repetitions of the motion were no longer disturbed (1041). Where animals as high in the scale as the ant and spider are concerned, it is possible that this process of getting used to a stimulus may involve rather a dulling of emotion than a disappearance of sensation. This phenomenon also is familiar in our experience, and may be called emotional adaptation.

That adaptation is itself adaptive hardly needs to be emphasized. As Jennings suggests, if the sea-anemone that contracts at the first ray of light were to remain contracted in steady illumination, it would lose all chance of getting food under the new conditions (508). The negative reactions ordinarily involve interruption of the food-taking process, and it is important that they should not be continued in response to stimu-

lation that is relatively permanent. Hargitt thinks that the loss of reaction to repeated shadows which he observed in marine worms may be an adaptation to the varying illumination caused by ripples at the surface of the water (386).

A very important psychological question concerns the permanence of the effects of adaptation. Sensory adaptation and lapse of attention to repeated or continuous stimuli, as these phenomena are met in our own experience, are not considered phenomena of learning at all. The former is purely temporary in its effects: the person who has become so used to an odor that he cannot smell it shows no effects of this experience half an hour later. The effect of familiarity on emotion and on attention is more lasting: one's loss of attention to a clock ticking in one's room may persist despite more or less prolonged absences from the room, although a sufficiently long absence, during which one encountered no ticking clocks, would cause the sound to be noticed again. The loss of emotional response to a familiar stimulus may persist for some time. Emotional adaptation and lapse of attention to continued stimuli may fairly be termed learning in proportion as their effects are more than temporary.

In many cases, the effects of adaptation on animal reactions last over a considerable interval between the stimuli. This seems to be increasingly the case, the higher the animal. Thus *Hydra*, which is only a *cœlenterate*, if it is allowed to reach full expansion after having contracted at a touch, will respond to the second touch just as it did to the first; the stimuli, to exert any influence on later reactions, must come in quick succession. On the other hand, in the responses of mollusks to shadows, the experiences of one day appear to extend their effects to the following day (720, 804, 806). Here we are dealing with a new type of modification by experience, though one which develops directly out of sensory adaptation; namely, the relatively permanent dropping off of useless movements.

§ 75. *Modifications Due to Relatively Permanent Effects of Stimuli*

In true learning, the conscious experience and the behavior of an animal suffer changes so lasting, relatively speaking, that they cannot be set down as due merely to adaptation of the sense organ, muscular fatigue, hunger, satiety, or any other variable physiological state of the organism. On the other hand, as we saw in Chapter II, the modifications must occur rapidly enough so that there is no time for actual changes in the animal's muscular structure to be produced. In animals which possess nervous systems, true learning is probably always the result of alterations in the connections between the elements of that system, such that the nervous process is able to pass easily in a direction where it originally encountered high resistances.

The fundamental law of all learning is the Law of Repetition, whereby when a nervous process traverses a certain pathway in the nervous system, it leaves the resistances in that pathway less than it found them. This is the law in accordance with which, when we wish to learn anything, we repeat it over and over, relying on the certainty that each repetition will make the next one easier. With this law in mind as an essential postulate, we shall survey the types of true learning found in the lower animals under the following four heads: (1) learning involving the dropping out of movements; (2) learning involving the formation of series of movements; (3) the recognition of landmarks; (4) learning involving the anticipation of movements.

§ 76. *Learning Involving the Dropping Out of Movements*

Among all the movements which an animal is capable of making, there are some which are closely connected with the great needs of its existence, and others whose connection with such needs is only indirect and casual. The general process

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of adjustment to environment which has made the animal what he is, has so ordered matters that the vitally important movements are in a state of especial readiness to be performed. The nervous resistances along the pathways leading to the muscles used in these movements are congenitally low. Such responses are what Sherrington (928, p. 229) has called "prepotent reflexes."

Now if we survey all the cases in which an animal learns by experience, we are obliged to conclude that on some principle of economy of energy, isolated movements which do not bring any consequences of importance to the organism tend to be dropped, and their places taken by a state of rest. This seems to be the law according to which we ourselves cease to pay any attention to our familiar surroundings. We cease to notice the ticking of a clock, although no adaptation takes place in the ear itself; we sleep undisturbed by the noise of the trolley cars which is distracting to our friends from the country. The spider experimented on by the Peckhams reacted each day to the sound of a tuning fork by dropping from its web until the sound had been repeated some half dozen times, but after the fifteenth day it would not drop at all (782). Piéron (804, 806) found that snails, while at first responding to shadows by withdrawing the tentacles, on successive days stopped reacting after fewer and fewer trials; and believed he could trace a parallel between the laws of this learning and those of human memory. There is no question in such cases of the reaction's being dropped off in favor of some other reaction. It is dropped off, as it were, by its own weight; simply because it is useless. This same principle seems to enter as a coöperating factor in cases where animals acquire a discrimination between stimuli. The apparent ability of sea-anemones to distinguish between real food and filter paper soaked in food-juice (see page 254) is, as we have seen, ascribed by some to sensory adaptation, but the experiments of Fleure and Walton (304), if their results are accepted, would indicate that true learning is involved. They

tested *Actinia* with a scrap of filter paper once every twenty-four hours, placing it on the same tentacles, which usually carried it to the mouth, where it was swallowed and later rejected. After from two to five days the mouth would no longer swallow the fragment, and in two more days the tentacles refused to take hold of it. Other tentacles could be "deceived" at least once or twice after this, but very soon manifested the inhibition. All traces of the learning were lost after from six to ten days interval. Another anemone, *Tealia*, learned more quickly than *Actinia*. Again, Herrick (408) found that catfish, when the barbels were touched with a bit of meat, immediately seized it. If a piece of cotton wool were used instead of the meat, they made the same reaction, but after this experience had been repeated a certain number of times they ceased to respond to the cotton, although they still took meat eagerly. The point which especially concerns us is this: "I rarely," says Herrick, "after the first trials, got a prompt gustatory reflex with the cotton." The learning persisted for a day or two. The axolotl learned in a similar way to discriminate between pieces of meat and pieces of wood (374). Hermit crabs, which when young try to take up their abode in all sorts of unsuitable objects, glass balls, for instance, later in life make no such efforts (263).

Whether or not a movement which brings no favorable results will be dropped off and a state of no movement will take its place depends on how strongly prepotent the movement is; upon the strength, that is, of the innate tendency to make it. In the experiments by Professor Bentley and the writer on color discrimination in the creek chub, our first method failed because it required the dropping off, as useless, of a strongly prepotent reaction, and the substitution of no response at all. Red forceps and green forceps, each containing food, were plunged one at a time into the water; the fish was allowed to get the food from the red forceps, but the green ones were withdrawn before it had a chance

to bite. The time which the fish took to rise and snap at the forceps was measured by a stop-watch, and in the course of 131 experiments the fish had not learned to rise to the green any less promptly than to the red. In other words, no tendency to drop off the useless movement of rising to the green was detected, although later experiments showed that the fish could distinguish between the two forceps. The movement of rising to and biting any small object in the water was so vitally important to the fish that it could not be dropped off (1036). On the other hand, White (1069), in her experiments on color discrimination in mudminnows, got the fish to do this very thing; they checked all response to green light when food was associated with red, although the two stimuli were presented successively. Fish have been trained to discriminate between real food and imitation food (bits of rubber or chalk), seizing the former and letting the latter alone (151).

Thorndike (969) successfully carried out this kind of training with Cebus monkeys: both of his subjects learned to come down to the bottom of the cage for food when the experimenter took the food in his right hand, and to *stay up* when he took it in his left hand, the food being withheld if the monkeys came for it in the second case. Cole (180) trained raccoons to climb up on a box for food when one of two differently colored cards was shown, and to *stay down* when the other one appeared, by not feeding the raccoons if they climbed up for the wrong card.

The dropping off of movements takes place with more speed and certainty if they are made to give place *not simply to a state of no movement at all, but to a movement of greater prepotency than their own*. This is the law governing the so-called "conditioned reflex"; if two stimuli each with its own motor response occur together, the less prepotent response will often drop out, and the more prepotent one become attached to both stimuli. Take for example the taming of an animal by feeding it. At the beginning of the process we may have two

stimuli, the voice of the trainer calling the animal, and the sight of food in his hand. Each stimulus has its response attached: the man's voice imitates the reaction of flight; the sight of food, that of approaching. Since these reactions are opposite and incompatible, the less vitally important one will be dropped off. Which one shall be prepotent would depend in this case on the animal's physiological state; if it is hungry enough, the flight reaction will yield to the food reaction, which will become attached not only to its original stimulus, food, but to the stimulus which at first called forth the flight response, that is, the trainer's voice.

Especially effective in thus causing the elimination of a movement is the *negative reaction* of withdrawal from injury. Thus if a movement *A* results in actual harm to the organism, the harmful stimulus thus produced brings about the negative response; and the negative reaction is as a rule prepotent over all others. The next time the movement *A* is initiated, the negative reaction is also initiated, and being prepotent, it is able to check effectively the performance of movement *A*. Thus we have the *dropping off of harmful movements*, a process which is in evidence whenever punishment is used in studying the learning power of animals. It also appears when a successful negative reaction permanently takes the place of unsuccessful ones. We saw in the first part of this chapter that when an animal is repeatedly subjected to a strong and harmful stimulus, it goes through a series of reactions, all directed to getting rid of the stimulus, until one is finally successful. Now if this process is shortened in successive trials, so that the successful negative reaction comes to be made at once and the unsuccessful ones are dropped off, we have a case where the dropping off is not simply of useless but of harmful movements (since the unsuccessful ones all result in a repetition of the harmful stimulus); the final state is not one of no movement, but of victory for the successful negative response. Van der Heyde (1006) placed ants on small twigs, from which they could escape only by dropping

to the ground. Of seven tested, one ceased on the second trial all useless running to and fro; two learned less quickly, two slowly, and one not at all. An interesting experiment which seemed to demonstrate this type of learning in the simplest group of animals was made nearly simultaneously by Stevenson Smith (1936) and by Day and Bentley (1940). A glass tube was drawn out until it was so fine that not more than one Paramecium could get through it. This tube was filled with water up to a certain point, and a single Paramecium, carefully isolated for identification throughout the experiment, was allowed to swim up the tube until the surface film was reached. The animal behaved towards the film as to any mechanical stimulus, darting backward, rolling over towards the side away from the mouth and swimming forward again. Since the tube was so narrow, this method, which ordinarily succeeds in avoiding obstacles, brought the animal against the surface film again. After repeatedly going through the same performance, the Paramecium varied its response and succeeded in turning completely around in the tube by bending its body double. On being put again into the same predicament, it gradually diminished the number of trials of the unsuccessful negative response, and arrived at the point where it almost immediately doubled over on striking the surface film.

Later, however, Buytendijk (1943) repeated these experiments and concluded that their results were due not to learning, but to the fact that paramecia when subjected to much mechanical stimulation, lose "tonus," that is, become limp and flexible; as can be seen when they are moving in masses of vegetable fibre.

If this were a case of learning, it would be one in which the movements dropped off are themselves negative reactions: a more important type of negative response is substituted for a less important one. In other cases, the suppressed reactions may be feeding reactions or other responses whose vital importance, though great, cannot compete against that of the

negative response called forth by their injurious effect in the special case. Learning by punishment is in most cases especially rapid. Its effect may be to inhibit altogether, for some time, a certain instinct. For example, the experience of receiving an electric shock when they seized a certain kind of food prevented frogs from feeding at all for several days (896). A toad which had swallowed a red ant avoided a spider and a fly as well as another ant on that day; the next day it accepted the spider but rejected the ant (141). Möbius in 1873 (691) made some experiments with a pike, afterwards repeated by Triplett (981) with perch, which illustrate the same phenomenon. The fish was kept in one half of an aquarium, separated by a glass screen from the other half, in which minnows were swimming about. The pike naturally dashed at them, and whenever it did so bumped its nose on the glass partition. After a considerable period of this sort of experience, the glass screen was removed, and the minnows were allowed to swim freely around the pike, when it was found that the latter's instinct to seize them had been wholly suppressed by the harmful consequences of such action. Here, again, the chances that a movement will be suppressed in favor of the negative response depends on how great the degree of its prepotency is. It was a rash conclusion on Bethe's (59) part to deny the learning ability of the crab because, although every time it went into the darkest corner of its aquarium it was seized by a cephalopod lurking there, it did not in six such experiences learn to inhibit its innate tendency to avoid light: further training would probably have been successful. Yerkes (1114) trained an earthworm, by giving it an electric shock when it followed its innate inclination for turning towards a darkened region, to turn away and towards the light.¹ The cockroach, as is well known, prefers darkness to light: Szymanski (951), however, succeeded, by giving it an electric shock when it ran into the dark part of a box, in educating it to turn back as soon as it reached the

¹ This experiment was much later performed by Heck (399).

edge of the darkened region, without waiting for the shock, and Turner (994) obtained similar results.

Blees (74) contrived to overcome the strong positive phototropism of *Daphnia* by an ingenious method. A single *Daphnia* was put in a glass tube, containing water and closed at one extremity. This tube was laid on the floor of a tank illuminated at one end, and was placed at right angles to the direction of the light; the *Daphnia* oriented and swam straight towards the light, and of course bumped against the wall of the tube. The number of such bumps was counted until the animal finally made its escape from the tube. In successive experiments this number diminished; the experiment was then tried with the tube directed about 135° from the light, and finally with it turned directly away from the light. In spite of the fact that this position required, for escape from the tube, movement in direct opposition to their positive phototropism, all the individuals tested made their escape with a diminishing number of bumps against the side walls. An obvious explanation for this behavior might be that contact stimulation was lessening or reversing their light tropism; this was disproved by the fact that immediately on reaching the end of the tube, the *Daphnias* oriented and swam towards the light.

When an instinct is thus completely suppressed by punishment, the conscious accompaniment of this modification in behavior is probably simply a change in the affective tone of the situation. Instead of being pleasant, it becomes unpleasant. In a human being, memory ideas might accompany the process: a human pike, for instance, might at the sight of a minnow recall clearly the bump on the nose and his consequent humiliation. But we can explain the pike's behavior just as well if, in accordance with Lloyd Morgan's canon, we assume merely that the sight of a minnow has become unpleasant to him: he has lost his taste for minnows.

Punishment has been the means in many cases of training animals to manifest their ability to discriminate between

stimuli. The desired end is of course to attach the negative reaction to those features in which the "wrong" stimulus differs from the "right" stimulus. For instance, an animal is being taught to choose a light rather than a dark passage, the two openings being side by side: when he enters a dark passage he gets an electric shock. It will be natural for him at first to attach the withdrawing reaction consequent on the electric shock to the sight of the whole apparatus. Whether he will shrink back from it or rush indiscriminately into either of the passages depends on the relative prepotency of his impulse to enter the passages and his impulse to withdraw from injury: in either case he makes no discrimination. The discrimination occurs when the withdrawing reaction attaches itself to the feature which distinguishes the dark passage from the rest of the apparatus, namely, its darkness. It is probable that in many cases the animal does not deliberately compare the light with the dark passage, but merely learns to distinguish the passage to be avoided from the rest of the situation at large. We should expect this to be the case where punishment is the only method of training used: the case would not be one of "white preferred to black," but of "anything rather than black."

Much of the experimental work on sensory discriminations and spatial discriminations has been performed by this method, as we have seen in former chapters. In other researches employing the method, the main interest has lain in the learning process rather than in the discriminative powers revealed by the results. It is evident that when punishment substitutes the negative response not for a total tendency, like the feeding instinct or the tropistic response to light, but for this tendency in connection with a particular stimulus, the punishment must be less severe. Buytendijk's toad after swallowing a red ant, lost much of his appetite for food in general; the next day his experience with the ant led to a discrimination between an ant and a spider. The effects of the punishment were weakening with time: to speak more exactly,

the feeding response was becoming prepotent once more over the negative response. We shall discuss later the influence of varying strengths of stimulus upon learning.

Cockroaches have been offered a choice between two compartments, with one of which an electric shock was associated; they thus learned to distinguish right from left (952).

The negative reaction to punishment is not the only one which may show sufficient prepotency to cause the dropping off of other responses. The feeding reaction, or any other innate response, may serve: thus *reward*, as well as punishment, is a method of training. For example (964), a freshwater snail, crawling after the manner of its kind upside down on the surface film of water, when food was brought in contact with the skin near the mouth, responded by chewing movements. A pressure stimulus produced no response, but when applied simultaneously with the food stimulus it inhibited reaction to the latter; thus it did actually occasion a change in the organism incompatible with and prepotent to the feeding response. After a time, however, not only did this effect wear off, but when the pressure stimulus was applied *alone*, the chewing movements were given. This is a perfect analogy to the conditioning of the salivary reflex in dogs by touch stimuli presented along with the sight of food. The taming of an animal by kind treatment illustrates both the simple dropping off of useless movements, the getting accustomed to a situation, and the substitution of movements more valuable to the animal; the tamed creature on the one hand learns to rest quietly in the presence of its tamer, instead of displaying alarm, and on the other hand to come for food or follow for companionship. A very pretty illustration of the overcoming of an innate response to light by the response to feeding was obtained by Wodsedalek (1084) on immature mayflies. These insects have an innate tendency to avoid light and to remain under stones in the water. By regularly feeding them on the upper surface of a stone the experimenter was able wholly to overcome this reaction, especially with one gifted individual.

After two months of training, "all that was necessary to bring the specimen up when it had disappeared from sight was to slightly jar the dish or the table on which the dish was located, and the insect would quickly come up to the upper side of the rock and make for its feeding place." Here again, the conscious aspect of the learning is probably a reversal of the emotional tone of the situation: originally unpleasant, it has become pleasant. Where the method of reward is used to train animals in discriminating stimuli, the influence of the reward is combined with that of the tendency to drop off useless movements. Cole's raccoons learned not only to climb up when the food signal was given, but to stay down when the no-food signal appeared. The rabbits studied by Miss Abbott and the writer (1035) were taught to push at a door carrying a piece of red paper, and to refrain from pushing at a door carrying grey paper. The original stimulus for the pushing was the odor of food which was in the compartments behind both doors. The "grey" door was always bolted on the inside, so that pushing against it was in vain; the "red" door opened freely so that the rabbits could get at the food. The actual securing of the food acted, along with the smell of it, to suppress all useless hesitations on the part of the animals and to make them more inclined to push the door at once; the grey stimulus acquired a tendency to lose its motor effect because the movements to which it gave rise were useless.

A *combination of reward and punishment* is often used in learning experiments. For example, a carp was offered a bit of worm attached by fine wire to a barbless hook: when he bit, he was pulled out of the water, taken off the hook, and thrown back, a total experience calculated to set up the avoiding reaction. Afterwards the carp avoided even free bits of worm, but only for a few tests: he then acquired the ability to distinguish between free worm and worm on the hook, by the following interesting method. Ordinarily on approaching a bit of food these fish suck in a current of water which brings them the morsel; the trained carp on the other hand ejected a

current towards it. This sufficed to lift the bit of worm a little from the ground if it was free, but not if it was attached to the hook (142). Clearly it is not easy to draw a sharp line between this type of condition and that where the "right" stimulus is associated with reward and the "wrong" one not with punishment but merely with a useless movement; if the tendency towards one kind of movement is very strong, the mere checking of it by an external obstacle may apparently operate as punishment. Take as an instance the experiments of Ven (1009) on the starfish: the animal was placed on a board and its movements restrained by rods between the arms and little wickets over the arms, one arm only being left free. The object was to train the animal to make no fruitless efforts in the direction of the restrained arms. The reward was return to the familiar aquarium. The results showed that in this case the restraints did not constitute an effective punishment, for the learning had to be accelerated by occasional pricks with a pointed rod. On the other hand, in the writer's experiments on color vision in rabbits (1035), a young rabbit of very nervous temperament was rendered unfit for further experiment simply by happening to push repeatedly at the wrong or closed door of a box. He had been working well up to that time, but from that time on he ran away whenever he was confronted with the experiment box.

An interesting problem in connection with this type of learning, where, of two movements associated each with its own stimulus, the prepotent one substitutes itself for the other one, is this: must the two stimuli be experienced together, or may they be experienced successively, and if so, how far apart in time? Yarbrough (1090) has investigated this problem with the rat by the following method. The animal is offered a choice between two pathways, right and left, both fairly long and presenting the same degree of difficulty. Having chosen a pathway, at some point in its course the rat gets an electric shock, and if he does not then turn round and seek the other pathway, he finds the exit door closed. The rats all learned

to turn round on getting the shock. An electric buzzer was then introduced, and sounded in various time relations to the shock. The noise of the buzzer became attached to the withdrawing reaction almost as readily if it was sounded one second before the shock as when the succession was immediate, but the learning time was greatly lengthened if the noise was given two seconds before the shock. The association was formed, however, when the interval was as long as six seconds. A similar association between light and sound was established more readily. Other experiments were performed to study the problem of backward association: when the buzzer in the training experiments was sounded immediately after the shock was given, the association between the noise and the withdrawing response was made almost as quickly as in the forward direction; but with an interval of more than one second the association was formed much less readily than when the noise (or light) preceded the shock in the training. As we shall presently see, the problem of "backward association" confronts us in explaining the formation of movement systems.

So-called "*puzzle-box*" experiments also depend for their training effect upon the combined tendencies to the survival, through their prepotency, of movements resulting in the satisfaction of an instinct, and to the dropping off of useless movements. The method has been tried with birds, rats, squirrels, cats, dogs, raccoons, porcupines, and monkeys. Thorndike, its originator, made some experiments of this type on chicks confined in pens from which they could be released by pecking at a string or some such object (965). Porter tested English sparrows with boxes containing food, which could be entered by pulling a string fastened to a latch, or by pushing the string into the wire netting with which one side of the box was covered (Fig. 12). The sparrows learned very quickly; one of them by the tenth test had left out all unnecessary movements (828). In later experiments a cowbird and a pigeon also learned to open a similar box. Before beginning the test the birds were accustomed to being fed in the box with the

door open. Their first success in opening the door lay in accidentally clawing or pecking at the proper point, and in later trials the action was simplified; thus the birds learned not to attack other parts of the box, to use the bill instead of the claws, and to stand on the floor beside the box instead of hopping upon it (829). In Rouse's test of the pigeon by the

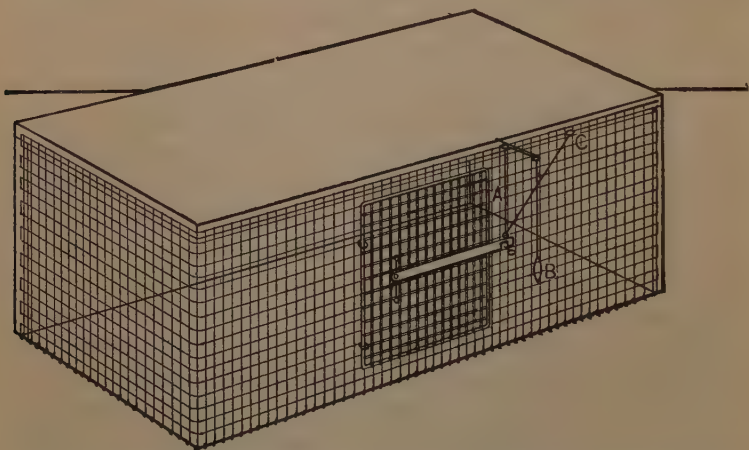


FIG. 12.—Puzzle box used in Porter's work on birds; *AB*, one method of attaching string to latch; *C*, a second method. In the first, the loop at *B* had to be pulled; in the second, the string had to be pushed in.

puzzle-box method, it showed less aptitude than that displayed by the English sparrow (882).

Small (932) tested his white rats with two boxes containing food. One could be entered by digging away the sawdust which was banked around the lower end of the box, if the digging was done in a particular place; the other, by tearing off strips of paper which held shut a spring door. The result of the earlier series of experiments with the first-mentioned box was that after an hour and a half on the first day one rat happened to dig in the right place and entered. The second day this rat took only eight minutes, and the thirteenth day only thirty seconds, to enter. With the second box there was

always a tendency to begin by digging, and even in the thirteenth experiment, where the rat got in by biting off the papers in fifteen seconds, she began by two strokes of digging. In a later test with this box the rat chanced to be extremely hungry, and dug violently for several seconds, displaying a blunting of the discriminative powers by hunger, analogous to that which we have found in very low animals. The rats were later trained to discriminate between the two boxes,

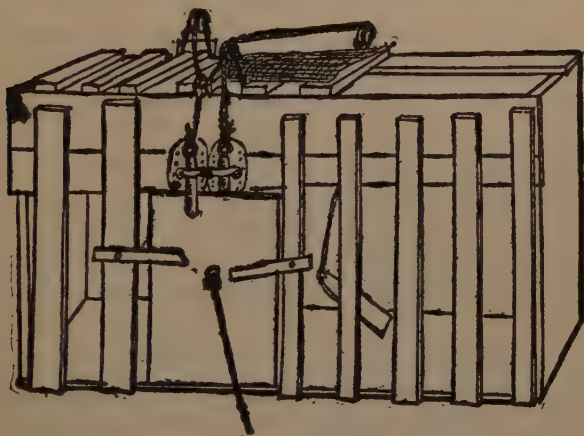


FIG. 13.—Puzzle box used in Thorndike's experiments on cats.

being sometimes presented with one and sometimes with the other.

In Thorndike's work on cats and dogs, the investigator placed the animals themselves in the boxes, and food on the outside, so that the problem was not how to get in but how to get out. The getting out could be accomplished in various ways, such as pulling a wire loop, clawing a button around, pulling a string at the top of the box, poking a paw out and clawing a string outside, raising a thumb latch and pushing against the door, and so on (Fig. 13). The animals, on being first put into the box, made all sorts of movements in their struggles to get out; the right movement was hit upon by

accident. Only very gradually, as the experiment was repeated again and again, were the useless movements omitted, until finally the right one was performed at once (965). Wesley Mills criticised these pioneer experiments of Thorndike's on the ground that the animals were under such unnatural conditions and in such an extreme state of hunger that they profited by experience more slowly than might otherwise have been the case (682); and this may have been to a certain

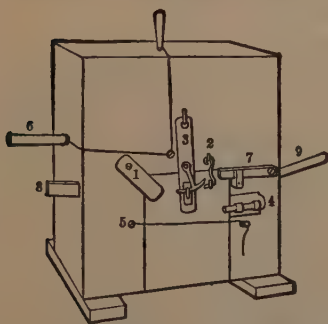


FIG. 14.—Combination fastening used in Kinnaman's work on monkeys. The figures indicate the order in which the parts of the combination had to be dealt with.

extent true. In testing monkeys with puzzle boxes Thorndike placed the food on the inside and the monkeys on the outside. He found a marked difference between the speed of their learning and that shown by the cats and dogs. "Whereas the latter were practically unanimous, save in the cases of the very easiest performances, in showing a process of gradual learning by a gradual elimination of unsuccessful movements and a gradual reënforcement of the successful one, these are unanimous, save in the very

hardest, in showing a process of sudden acquisition by a rapid, often apparently instantaneous abandonment of the unsuccessful movements and selection of the appropriate one, which rivals in suddenness the selections made by human beings in similar performances" (969). Kinnaman further complicated the box tests with his *Macacus* monkeys by constructing "combination" fastenings, which required the performance of a set of actions in a certain order, and found that these were mastered by the animals (540) (Fig. 14).

Cole's (180) work on the raccoon indicates that in speed of learning this animal stands "almost midway between the mon-

key and the cat," while "in the complexity of the associations it is able to form it stands nearer the monkey." The raccoons, like the monkeys, learned combination locks, although they did not learn to perform the various movements involved in a definite order. They showed an interesting tendency to skip at once to the movement that immediately preceded the opening of the door. The porcupine also proved gifted with the ability to learn combination locks (886), while the squirrel's puzzle-box exploits were limited to boxes which could be entered by the simple process of digging in sawdust (1125). The learning of combination locks probably involves the formation of systems of movement, as well as the dropping off of useless movements; the process of system formation will be discussed in a later section.

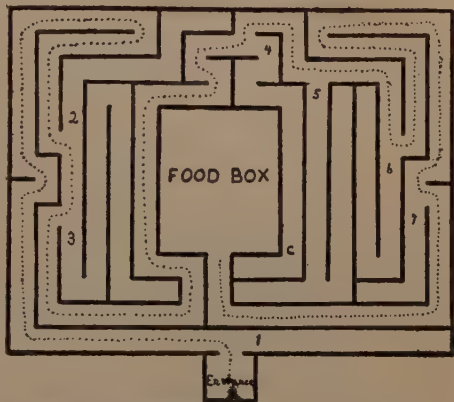


FIG. 15.—The Hampton Court maze.

The building up of systems of movements is an important part of the learning process in another method of studying the intelligence of animals, namely, the *labyrinth* or *maze method*. In the typical form of this method, food is placed at the end of a pathway involving a number of turnings, in which it is possible to make errors of two sorts: (a) taking a longer instead of a shorter route, (b) entrance into *cul-de-sacs*. The animal has to learn to run to the end of the path and secure the food in the shortest possible time, or by the most direct route. His progress in learning may be measured either by the total time he consumes in running the path in each trial, or by the number of errors he makes, or by the total dis-

tance he runs. The method in its developed form was first used by Small (933) in experiments on white rats, and is especially adapted to an animal so active as the rat. Small used a very complicated maze, a facsimile on a small scale of the one to be found in the grounds of Hampton Court Palace (Fig. 15). Such mazes, with high box walls, were a frequent feature of old gardens. Much simpler mazes have been used with other animals. Where a maze consists of only two passages, requiring the animal to learn merely a single turning, the method may be practically merely a discrimination method; thus Yerkes's (1114) training of the earthworm made use of a maze with two passages only to choose between, a light and a dark one. In a pure maze experiment, however, there is no way of distinguishing between the passages except by experiencing the consequences of following them. Thus the crayfish was tested by the use of a maze with a single choice of paths. One end of the box communicated with the aquarium; about halfway down the length of the box a partition put in longitudinally divided it into two passages, one of which was closed at the end by a glass plate. In sixty trials the animals, which had originally chosen the correct passage 50 per cent. of the time, came to choose it 90 per cent. of the time. A second series, with a single animal upon which more tests a day were made, resulted in the formation of a perfect habit in two hundred and fifty experiments. The glass plate was then shifted to the other passage, and the crayfish was naturally completely baffled for a time, but succeeded in learning the new habit (1122). The crab *Carcinus granulatus* made progress in learning to traverse a labyrinth with two points where a choice of path had to be made, but did not wholly master it in fifty trials (1097). For both the crab and the crayfish, the experience of getting back into the water was the influence relied upon to eliminate the useless movements; the slow learning of these animals indicates that the method was not well adapted to them.

The freshwater snail *Physa*, which learned easily to asso-

ciate the feeding reaction with a touch stimulus, could not master a maze involving only a single choice, the reward being to reach the surface of the water and get air, and the punishment being an electric shock (964). A land snail did learn a maze with one turning (346). Ants showed some ability to learn a maze with several turning points, following the proper course even when their smell trail was obliterated (295). Cockroaches displayed progress in learning fairly simple mazes (995, 273); fish have learned very simple ones, but have not been tested in complex mazes (966, 956). The green frog took a hundred trials to learn a maze with two choices: the toad's ability appeared about the same (1098, 140). Turtles learned a maze with four blind passages, containing an ascending and a descending inclined plane: the process of dropping off useless movements was observed very prettily in connection with these planes. The turtles had to turn around as soon as they had reached the bottom of the descending plane. They soon began to make the turn before they got to the bottom, and finally to throw themselves over the edge as soon as they reached the top (1094).

Some of Thorndike's early experiments on chicks (965) involved a very simple form of the labyrinth method, in that the chicks, confined in small pens, could escape by running to a particular spot or up an inclined plane. Porter (828) found that the English sparrow quickly learned the Hampton Court Maze, and that the vesper sparrow and cowbird learned a simpler form in twenty or thirty trials (829). Various European songbirds acquired the Hampton Court Maze, and pigeons have proved good maze subjects (888, 882).

White rats observed by Small learned the Hampton Court Maze, in nine experiments made at intervals of two days, so well that they committed only two errors in the ninth test, but the significance of this time is obscured by the fact that the rats were allowed to run freely about the labyrinth every night (932).

In Yerkes's (1113) study of the Japanese dancing mouse, the reactions to irregular and to regular labyrinths were compared, and it was found that a maze of the latter type, that is, one where left and right turns alternated, was more quickly learned and more perfectly mastered than an irregular one. Kinnaman (540) taught two *Macacus* monkeys the Hampton Court Maze.

Perhaps the most puzzling problem in the psychology of learning is that of the dropping off of *useless* movements. That harmful movements should be dropped off, we can explain by the general law of the conditioned reflex, that when two stimuli, each with its own reaction, occur together, the more vitally important response tends to survive at the expense of the less important one: a harmful stimulus produces a negative response, which it may be supposed regularly tends to be prepotent and thus to substitute itself for the response that led to it. But in maze-running such wrong movements as taking a longer rather than a shorter path do not lead to any negative reactions; and the obviously prepotent response of eating occurs so long after the early errors in the maze that it is hard to understand how any conditioning process can occur. Thorndike (965) said that the successful movements were "stamped in" by their *pleasant consequences*, at the expense of movements lacking such consequences; but both the shorter and the longer maze paths have pleasant consequences. Watson (1051) laid especial stress on the fact that the successful movements in puzzle-box and maze experiments have the advantage of *frequency* of performance. The successful movements are always performed, in every maze experiment, simply because the experiment continues until they are performed; there is no such necessity that any particular unsuccessful movement should be performed in every experiment. Thus the successful movements, Watson thinks, owe their survival to the law of repetition. It is probable that their inevitable performance once in each running of the maze may be a factor aiding their survival, although quite con-

ceivably, as Thorndike¹ has suggested, many unsuccessful movements may actually be oftener performed, owing to the fact that they may be repeatedly tried in the same experiment. Peterson (787) points out that when an animal arrives at the mouth of a blind alley that has been entered before in a given experiment, both frequency and recency would operate to make it enter again. Watson goes to the extreme of trying to reduce all learning through the dropping off of movements to the influence of the frequency with which the successful movements occur. This can be done only by ignoring such examples of learning as those where the frog ceased in one or two trials to snap at harmful food, or where the spider learned not to disturb itself at the sound of a tuning fork. Frequency cannot be a factor of importance here. Such cases show that there do exist in animals tendencies (a) to abandon movements which have no consequences of importance to the organism, and (b) to eliminate even movements that are important in favor of movements that have greater importance.



FIG. 16.—Ground plan of circular maze, showing the position of the errors studied.

It has been argued that if the shortening of the maze-running is due to the fortunate consequences of the successful movements, then the errors which should be earliest dropped off are those at the latter part of the course, which come nearest in time to the final success, usually the obtaining of food. Hubbert (474), working with the circular maze, Fig. 16, did

¹ Jour. Animal Behav., vol. 5 (1915), p. 465. Cf. also Hamilton.

not find this to be the case, although Carr's (156) later analysis of her data found them actually to show a dropping of errors in the order 6, 5, 4, 3, 2, 1, the number 1 indicating the first possible error on entrance. Vincent (1019) reports the errors near the food box earliest eliminated. But apparently, as Carr concludes, the conditions are complicated, and the influence of food satisfaction does not alone determine the order of elimination. Peterson (787) points out that Watson's frequency principle, while as we have seen it cannot explain the elimination of errors in general, would help to account for early elimination of those nearest the food-box.

Various researches have been made on other factors determining the order of elimination. Dashiell (230) finds that a blind alley opening straight ahead is more likely to be entered than passed, in the ratio 5: 3; this looks like a disinclination to turn on the animal's part, but on the other hand Hubbert and Lashley (475) report that rats have a stronger tendency to enter a doorway than to pass it. In my own observations I have found individual mice differing in this matter: some have a preference for straight runs and others an inclination to turn every corner they come to. There is disagreement among experimenters as to whether a short *cul-de-sac* or a long one is sooner eliminated. Peterson (788) reports that the short ones are dropped first. De Camp (242), however, used an apparatus offering only two paths to the food-box, so arranged that their relative length could be altered: the rats distinguished and preferred the shorter to the longer path even when the ratio was as small as 1:1.1, and Kuo (567) also found that a longer path was eliminated earlier than a shorter one. White and Tolman (1068) suggest that Peterson's opposite result was due to the fact that his short alleys were very short and straight, so that the rat could see the end and perhaps note a difference of air pressure: using short alleys with elbows in them and somewhat longer than Peterson's, they found that these were eliminated later than the long ones. It has been shown that the time factor is

essential in the preference of an animal for a shorter path. When the two paths are of equal length, but the rat can be detained in the middle of each for varying periods of time, that path will be chosen which has involved the shortest delay (890).

A fact that emerges from nearly all recent work on the maze is that the animal, having found food at the end of the maze path, almost immediately acquires an *orientation in the general direction of the food*. Needless to say, the error from smell is supposed to be eliminated; whether it always is, seems to the writer doubtful. The earliest errors to be dropped are those involving returns towards the starting place (788, 1028). Dashiell finds that the exit from a blind alley opening straight ahead is more likely to be in the forward than in the reverse direction in the ratio 3:2, and the probability in the case of a blind alley opening at the side is 3:5 (230). Warden (1028) reports that blind alleys out of the general direction of the right path are dropped sooner than those in its direction. Hubbert and Lashley (475) cite general orientation to the centre as accounting for the elimination in the circular maze of those errors which consist in running past the right opening.

End.

§ 77. *The Formation of Systems of Successive Movements*

We have now to consider another type of learning, which seems on the face of it diametrically opposed to that of the dropping off of movements. In this type, the movements which an animal successively makes become organized into a series. No movement of the series is dropped out as a result of the learning, but the oftener the series is run through, the more rapidly it is performed. It is evident, if we consider our own learning processes, that many of them are of this type. When we say the alphabet or the multiplication table, the learning process has not involved the dropping out of any of the movements. It would profit us little to pass im-

mediately from A to Z, dropping out the intervening movements, or to skip at once from the first to the last stanza of a poem. We find in such cases that repeated performance of the series of movements results in two changes. First, the movements follow each other more rapidly: this can be explained by the law of repetition, according to which the oftener the nervous process traverses a certain pathway, the less resistance it encounters. Secondly, the movements of the series no longer need outside stimuli, but apparently each movement supplies the stimulus for the next. When one is playing a piece of music for the first or second time, each movement has to have the stimulus of the notes on the page; when a piece has been long practiced, each movement sets up the next one "automatically." This really means that as one movement is performed, the sensory processes occasioned by the contraction of the muscles involved excite the motor pathway for the next movement. The stimulus for one movement is the kinæsthetic excitations received from the preceding movement. The truth of this is evidenced by the fact that if we break down in playing a certain passage, we can recover ourselves by going back a little, so as to get the proper kinæsthetic stimuli.

It is clear that this type of learning might function in learning a maze path: here we have to deal not with the acquiring of a single "successful" movement and the dropping off of all others, but with the establishment of a whole series of successful movements, which must be performed in a certain order. There is evidence that it does function. For example, take experiments where rats which had learned the maze from its beginning were started at points further along: they could not pick up the true path with any speed until, in running back and forth, they chanced to make two or three correct turnings. This set off the remainder of the maze-running process precisely as playing over the preceding passage would enable a pianist to proceed beyond the point of a breakdown. Similarly, when the maze was shortened by removing a section

from its middle, the rats ran against the ends of the shortened passages; when it was lengthened by elongating certain passages, the rats tried to make the turns at the old points (164).

Maze experiments are not the only observations on animals that reveal the existence of successive movement systems, or "kinæsthetic memory." If Piéron (793) is right, some species of ants are aided in their return to the nest by repeating all the turnings they took on the outward journey. Watson reports the following observation on the terns of the Tortugas. On an occasion after he had trained one of these birds to use a nest raised a hundred centimeters above the ground, he moved the nest a hundred centimeters to the eastward; the bird, returning, hovered "in space, attempting to adjust to the nest in the air at its former position and height" (1049, page 226). Rockwell (871) relates that a ground squirrel had made inside a cabin, a nest which it was accustomed to reach by climbing up the leg of a cot that stood in one corner of the cabin. When the cot was removed, the squirrel, entering the cabin, ran to the place formerly occupied by the cot, and went through the motions of trying to climb the non-existent leg.

A freshwater snail (239), kept in a cylindrical glass tank, used to crawl up the wall to the surface of the water and through its siphons fill its lung with air, after the fashion of aquatic snails. The level of the water was raised. The snail was observed to crawl up to the height at which it had been accustomed to find the air; pause, and tap about with its siphons as if in search of the missing air stimulus.

These look like cases of pure movement systems, dependent wholly on kinæsthetic stimuli. A number of experiments with the maze indicate that during the learning process and before it is complete, *other stimuli* than kinæsthetic ones play a part. This indeed would be only natural, for in ordinary life the cases where no stimuli operated other than those provided by an animal's own movements would be exceptional. The original maze situation, as constructed by the old landscape gar-

deners, owed its amusing character to the fact that it put the human subject in a situation where he could use none of his external senses, and so could learn his path only by the slow operation of kinæsthetic memory. Of course, if external stimuli are introduced into a maze path, the experiment becomes in part a discrimination experiment. Thus Vincent's (1016-1018) experiments show that a maze in which the true path was painted black and the wrong path white, or *vice versa*, was learned more quickly than an ordinary maze; that one in which the true path was smeared with beef extract and cream cheese alternately (the two odors being used to prevent olfactory adaptation) gave a greater total accuracy; and that in a maze without sides, that is, an elevated pathway, the rats were much disturbed by the loss of the accustomed contact with the walls. Different animals are undoubtedly unlike in the use they make of sensory cues. The frog studied by Yerkes (1098) in a very simple labyrinth showed a disturbance in its habit when red and white cards placed on either side of the point of choice were interchanged. Rouse (882) found that the pigeon could make use of auditory cues. He arranged to have an electric bell rung whenever the bird entered a wrong alley, and a wooden bell sounded when they emerged and took the right course. After they had learned the path under these conditions, the two sound stimuli were interchanged, and the result was a certain amount of confusion on the part of the pigeons. The function of such outside stimuli introduced at critical points in the maze will be discussed later. Their effectiveness varies with the type of animal used: when Small placed red wooden pegs, at each division of the paths, in the middle of the correct path, rats were not helped in learning the maze (932). In Vincent's experiments with rats, it will be remembered, the visual clue that proved helpful was a black floor which was continuous throughout the correct path, rather than an isolated landmark at turning-points. Allen's (6) guinea-pigs did not alter their behavior when the position of colored cards in the maze was

changed. Different kinds of animals analyze their environment in different ways, as we have seen in § 72.

To the ordinary kinæsthetic processes in the labyrinth a new factor was added in some experiments where a maze with the entrance at the center, from which four paths led at right angles to one another, was inclined at an angle at 30° . The path leading to the food-box was that towards the top of the incline, so the rats had to learn to run up, which they did only imperfectly (233).

It appears that stimuli from *outside* the maze must also be reckoned with in the formation of the maze habit. The most extensive study of such influences is that by Carr (157-159). He investigated, first the effect of altered conditions before the rat, which has previously learned the maze, begins a particular run; such changes as altering the route by which the rat is carried from the living-cage to the maze (no effect), whirling the animal round before putting it in the maze (no effect), altering the position or the orientation of the living-cage (here the results were conflicting and puzzling). Secondly, he observed the effect of changes introduced while an animal was making its run, such as covering or uncovering the maze, increasing or decreasing illumination, changing the position of the experimenter, rotating the canvas cover of the maze, rotating it when one of its curtains was up, changing the position of the maze in the laboratory without altering its orientation to the points of the compass, and rotating the maze. Here the factor which seems to have determined the influence of the altered conditions was whether the environment was *uniform* or *heterogeneous*. Thus a change like covering the maze or rotating the canvas top did not disturb the rats; but turning on an electric light, covering a window, or rotating the canvas top when one of its curtains was drawn up; in other words, changing some object in the environment rather than the whole environment uniformly, did affect them.

It is clear that the problem of perception, which was discussed on pages 238 ff., is involved here. Those psychologists

who like Volkelt emphasize the influence of the total pattern of experience in all perception, will see in the influence of these environmental factors on maze-running an instance of the truth of their doctrine. But another interpretation can be put on such disturbance by outside factors; namely, that they are due to *fright*; to distraction and uneasiness at the appearance of something new, or merely to the tendency to pause and *examine something new*. Convincing testimony to the truth of this interpretation is furnished by some of Carr's observations, just quoted. If a cover was placed over the maze while the rat was running it, the rat was not disturbed. Yet the total pattern of the rat's consciousness was markedly altered by this change. But the change consisted in substituting for a heterogeneous environment of things a homogeneous environment. The appearance of a new thing might occasion fear or curiosity; the disappearance of all things into a uniform covering would not.

Two other experimental observations of the influence of environmental conditions may be noted. Szymanski (956) trained a group of rats in a maze where all the blind passages were closed, so that errors were impossible. He found that these rats appeared not to know the maze when the blind passages were opened: the most natural explanation of this is that the suddenly opened passages appealed so strongly to their exploring tendency as to distract them from the true path. Hunter (485) constructed what he called a temporal maze, in which by shifting partitions in a path running around an oblong the rats were made to take left and right turns in the same order of succession as was required in a more complicated maze. He found that thus having established a sequence of turns did not enable the rats to run the more complicated maze, and concludes that the kinæsthetic theory of maze running is incorrect. But here again we need only suppose that the different environmental conditions distracted attention. As a matter of fact, Hunter's temporal maze did not provide exactly the same sequence of turns as the other maze.

Curious, and as yet unexplained, are the effects of altering the relation of the maze to the points of the compass; that is, *rotating* it. Watson (1047) was the first to note that this disturbs the running of a familiar maze, and Hunter (477) found that some of his pigeons were disturbed while others were not: he concludes that the latter were guided by cues within the maze and the former by cues from without. Carr (157) has done the most extensive work on this problem. That disturbance should occur when the environment is heterogeneous can easily be explained by the distracting effect of the altered series of external stimuli which the rat meets in its course. Carr's observations on adaptation to rotation are interesting. If the rat learned the maze successively in all four altered positions, 45° , 35° , 225° , 315° , by the time a fifth position was reached all traces of disturbance had disappeared. The rat had become, in other words, so used to a varying environment that all reactions to the environment dropped off. Experiments on blind rats and rats in which the sense of smell had been eliminated by operation showed that this process of adaptation occurs by vision.

But disturbance by rotation of the maze occurs even when the environment is homogeneous, that is, when the maze is covered and the cover is rotated with the maze; and under these conditions adaptation does not occur. No reason appears why animals should be disturbed when no factor of their environment either within or without the maze except their relation to the points of the compass is altered.

In connection with the relation of the dropping off of useless movements to the organization of successful movements into movement systems, it must be noted that useless movements not infrequently get organized into movement systems, and thus their elimination is delayed. Animals in running a maze form habits of going wrong which greatly interfere with the reduction of their time records. In the case of some salamanders which the writer vainly tried to teach a fairly complicated maze, each individual acquired quite an elabo-

rate habit of making wrong turnings, and remained true to it for some time. Van der Heyde (1006) notes this in the maze-running of ants. Whenever the situation does not involve strongly prepotent movements, whenever, that is, the "motive," though always present, is weak, the tendency of movements to organize into systems may take the place of the tendency to drop off the unnecessary ones. Such an influence as this is very likely one reason why errors in the maze are not eliminated in the exact order of their distance from the final, beneficial, and pleasurable goal.

The conscious accompaniment of the formation of successive movement systems is, in our own experience and probably in that of an animal, the diminishing of attention to outside stimuli, and the disappearance of such emotional states as uncertainty and the unpleasantness of errors; a feeling of confidence and security replacing them.

There is an alleged case of learning on the part of certain marine animals which, if it exists, probably belongs under the head of the formation of successive systems. This is the acquisition of *rhythmic reactions*, to stimuli which occur at equal time intervals, and the persistence of such rhythms when the stimuli have ceased to act. Marine snails, sea-anemones, annelid worms, and hermit crabs show changes in the direction of their responses to light and to gravity which correspond with the state of the tides: the sea-anemone, for instance, opens at high tide and shuts at low tide. Now certain French observers, Bohn (96, 106), Piéron (800), and Drzewina (261) report that when the animals are removed to the aquarium, they continue to show fluctuations in their light and gravity reactions at the times of high and low tide, although of course the actual stimuli which the tide gives them, for instance the mechanical jarring of the waves entering their pool as to the tide rises, are now wholly lacking. No American observer has been able to show such a continuance of the tidal rhythm in animals removed from direct tidal action (348, 398, 707, 757). Richter (864) reports that

rats accustomed to being fed at certain intervals showed activity at these intervals even when food had been withdrawn. These phenomena suggest analogies from our own experience; for instance, there is the case of "habit hunger." We feel hungry at the time of day when we are accustomed to be fed; if we do not get food at this time, in half an hour or so the hunger sensations disappear, and we can go quite comfortably without food for some time longer. The hunger sensations are due to movements of the stomach; now these movements were originally induced by the presence of food in the stomach at a certain time. They have apparently become a part of a system of internal, organic movements, so that when these internal processes have continued for a length of time equal to that which usually elapses between meals, they produce the stomach contractions, in the absence of the original stimulus, the food. Thus the case seems to be like that of the running of the maze by a thoroughly practised animal; each act is the stimulus for the next, and outside stimuli are unnecessary.

CHAPTER XI

THE MODIFICATION OF CONSCIOUS PROCESSES BY INDIVIDUAL EXPERIENCE (*Continued*)

§ 78. *The Recognition of Landmarks*

A TYPE of learning which stands by itself is that involved in the homing of certain animals. As we have seen, the evidence is conclusive that solitary wasps guide themselves back to the nests they have made by "recognizing" certain visual peculiarities of the surroundings. They are confused if the appearance of the nest or its vicinity is altered. On first leaving the nest in search of the prey with which to stock it, as food for the larva, they make an elaborate flight with many turnings in and out about the immediate neighborhood, which has been appropriately termed a locality survey. Now when the wasp has found and secured the caterpillar or spider which she seeks, she retraces her flight apparently with the guidance of the visual landmarks she noted on the outward journey. No one, it is true, has yet actually determined the homeward flight of the wasp in its relation to landmarks, but the probabilities are that such is her method of procedure. The peculiarity of such learning is that it *does not depend on repetition*. The wasp makes but one nest in a given situation, and in the case of certain species at least she makes but one flight in search of food and but one homing flight. She then makes a new nest in a new locality, impresses new landmarks upon her memory, and is guided in her next homing flight by the new and not the old landmarks. The learning is essentially rapid and temporary. Where, as for instance with the honey bee, the nest remains permanently fixed in one locality, guidance by visual landmarks does not differ from the ordinary

types of learning where the process is gradual, where useless movements are eliminated and useful movements organized into systems. We are still in possession of too few detailed observations on the homing flights of the wasp to draw positive conclusions as to the nature of the learning process here.

Still more mysterious, in fact, thus far more puzzling the more data we get, are these homing processes which seem to involve memory of direction, not based either on visual, tactual, or kinæsthetic data. The limpet wanders from its position on the rocks, and returns to it. The supposition formerly was that tactual and kinæsthetic recognition of the contour of the rocks over which it passed was probably its guide, but the careful observations of Wells (1058) on the animals in their normal habitat show that they do not actually retrace their paths. As soon as the rising tide wets them with spray, they leave their places, crawl in ovals, and turning almost but not quite completely around at one point begin their return journey. The ovals increase in size in successive foraging trips during the period of high tide. This behavior seems to correspond closely to the homing of Algerian ants as described by Cornetz, and to involve a mysterious sense of direction. Arey and Crozier (11) describe similar behavior in the limpet *Onchidium*, and explain it by "some internal condition simulating memory of the position of the nest in terms of the surroundings, but independently of guidance by the mechanically directive features of the environment." Herrick (410) has made some experiments on the legendary ability of the cat to find its way home. He reports that when carried long distances away and liberated in strange territory the cat seems to have a "direction constant," not dependent on memory: it does not retrace its path, but orients directly for home. It can do this even when anæsthetized on its outward journey.

§ 79. *The Memory Idea*

It is sufficiently clear that animals possess the power of learning, in the sense of a power of reacting differently to

a present stimulus because of their past experience with it. Probably not a single animal form is so low that it lacks this power. But there is another type of learning, of which human beings make much use, whose existence in animals we have yet to investigate; namely, the ability to recall a mental image of an absent stimulus, a memory idea. A dog shows clearly that he remembers his master, in the sense of modifying his behavior in his master's presence because of his previous experience. Can we be sure that he has remembered him in his absence; that he has had a memory image of his master?

Most people, following the tendency to humanize animals and ignoring Lloyd Morgan's canon, interpret as evidence of memory ideas certain features of animal behavior which are susceptible of much simpler interpretations. Dogs and cats, for instance, are supposed to dream because they snarl and twitch their muscles in sleep; but as Thorndike (1965) has pointed out, such movements may be purely reflex and unaccompanied by any consciousness whatever. A dog shows depression during his master's absence, but his state of mind may be merely vague discomfort at the lack of an accustomed set of stimuli, not a clear idea of what he wants; as when we *feel* that we have forgotten something or that something in our environment has been altered.

We shall first consider certain pieces of evidence which indicate that in many of the lower animals the existence of memory ideas is highly doubtful. Later, we shall note certain testimony in favor of their existence in the minds of some animals, although probably with a very restricted function.

One argument from which we may conclude that animals do *not* make use of memory ideas where human beings would, is derived from the *gradual character* of the dropping off of useless movements in experiments of the puzzle-box type. A human being who had once hit by accident on the right way to open a lock could hardly fail, on being confronted with the lock a second time, to recall an idea of the successful move-

ment and to perform it at once, without wasting time and effort on unnecessary movements; but a dog or a cat makes almost as many random clawings and pawings the second time as the first, and only gradually omits the irrelevant motions.

In the next place, animals very generally show a *lack of ability to imitate other animals when the imitatee is not actually present* before them: that is, they cannot imitate by remembering the other animal's movements. Imitation may be, as various authors have pointed out, of at least two different types. The first has been called instinctive imitation, and is common among social animals. It occurs when the sight or sound of one animal's performing a certain act operates apparently as a direct stimulus through an inborn nervous connection, to the performance of a similar act by another animal. "If," says Lloyd Morgan, "one of a group of chicks learns by casual experience to drink from a tin of water, others will run up and peck at the water and will themselves drink. A hen teaches her little ones to pick up grain or other food by pecking on the ground and dropping suitable materials before them, the chicks seeming to imitate her actions. . . . Instinctive actions, such as scratching the ground, are performed earlier if imitation be not excluded" (704, pp. 166-167). Imitation in this sense is hardly so much a method of learning by experience as a method of supplying experience. An animal may perform an act the first time because, through inherited nervous connections, the sight of another animal's performing it acts as a stimulus. But it will continue to perform the act, in the absence of any copy to imitate, only if the act is itself an instinctive one, like drinking in birds, or becomes permanent by reason of its consequences, just as would be the case if its first performance had been accidental rather than imitative. As a matter of fact, instinctive imitation seems usually to be concerned with actions themselves instinctive. The tendency at present is to deny that imitation is an instinct; even McDougall, who is in general inclined to lay much stress on instinctive factors, resolves this

type of behavior into the tendency to follow and the "primitive sympathetic reactions" (625). What concerns us here is merely that these cases of repetition by one animal of another animal's acts, since they occur while the latter is still acting, do not indicate the presence of memory ideas.

Inferential imitation, or what Morgan calls reflective imitation, is a different affair. It is the case where an animal, having watched another one go through an action and having observed the consequences, performs the same action although the copy is no longer before it. Such behavior naturally suggests that it is accompanied by some kind of memory idea of the act that is imitated. Now Thorndike, in his experiments on chicks, cats, and dogs, found no evidence of this type of imitation. A cat put in a puzzle-box did not learn the way out any sooner for watching, even repeatedly, the performances of a cat that knew how to get out (965). With monkeys, Thorndike's most extensive tests were made to find whether the animal would learn to open a box from seeing the experimenter himself do it, and his results were again, on the whole, negative (969). Small's white rats also showed no ability to profit by each other's experience in this way. One of each of the pairs first experimented on solved the problems presented; the other, instead of either attacking them for itself or learning by watching the successful one, contented itself with stealing the food secured by the latter (933). Imitation, according to Yerkes, plays no considerable rôle in the learning processes of the dancing mouse (1113). Where an animal is not at all helped to the solution of a problem by watching another animal solve it, we are justified in concluding that if it can recall memory ideas at all, it does not make use of them in a situation where a human being would certainly do so. *and*

The lack of ability on an animal's part to postpone reacting to a stimulus is another evidence of inability to make use of memory ideas. The very ingenious method by which such ability may be studied was the device of Hunter (478). It

has been termed the Delayed Reaction Method, and its general plan is as follows (Fig. 17). A light is shown for a few seconds in any one of three directions from the animal, which is restrained from reacting. After the light is turned off and a certain time interval has elapsed, the animal is released, and if it goes in the direction in which the light appeared,

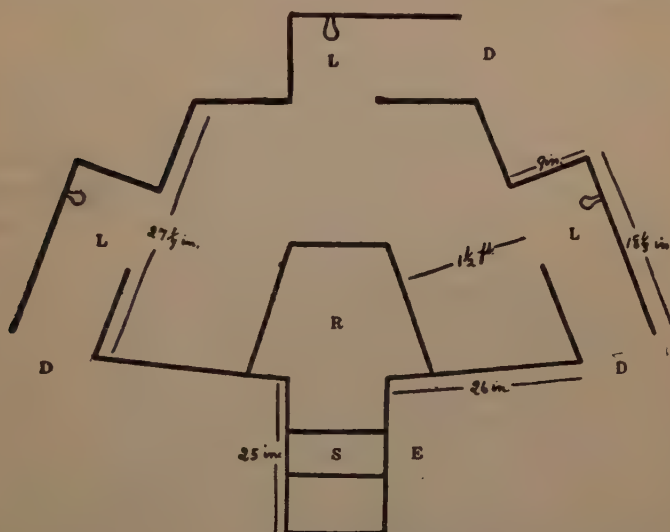


FIG. 17.—Ground plan of Delayed Reaction box used with raccoons. *R*, release box; *DD*, sliding doors controlled by strings from *E*, experimenter; *LL*, light bulbs. (After Hunter).

it receives food. Now white rats could succeed in running in the proper direction when the delay between the disappearance of the light and their release was not more than ten seconds, but only in case they pointed their noses at the light when it appeared and remained motionless in this position during the interval. Clearly we get no indication from such behavior that the rat is able to recall a memory image of the light. His failure to run in the right direction when he did not keep his nose pointed in the right direction plainly sug-

gests the absence of such ideas as influences on his behavior. Dogs and cats (1089) also depended for success on the maintenance of a fairly constant bodily orientation during the delay interval.

Again, the *nature of the errors* which animals occasionally make in experiments strongly suggests the absence of memory ideas. Thus the two rats which learned the Hampton Court Maze under Small's (933) tuition both continued, after they had reached their highest point of excellence in running the maze, to take the wrong turning at the outset. Precisely this error would have been, probably, the first one eliminated in the learning of a human being, who would be able to recall some kind of memory idea of the first turning owing to its especial hold upon attention. Further, the *way in which instinctive actions are performed* by animals often indicates that ideas are not present as they would be to a human being's consciousness. Human beings do some things from instinct, but the doing of them may be accompanied by ideas; a mother's care for her child involves ideas of the child's happiness or suffering, and of its future. Enteman's account of the worker wasp which, lacking other food to present to a larva, bit off a portion of one end of the larva's body and offered it to the other end to be eaten, suggests a peculiar limitation of ideas in the wasp's mind, at least while this particular function was being performed (278). The cow, which had lamented at being deprived of her calf, and on having the stuffed skin of her offspring given to her, licked it with maternal devotion until the hay stuffing protruded, when she calmly devoured the hay (701, p. 334), had perhaps experienced some dim ideas connected with her loss, but certainly her consciousness was more absorbed by the effects of present stimulation and less occupied with ideas than a human mother's would have been.

Thorndike (965) was the first to point out how scanty is the evidence in favor of the possession of ideas by the lower animals. In addition to the fact that his dogs and cats

dropped off their useless movements so slowly, he adduced the observation that while after a time the cats which had been caused to enter a puzzle-box and let themselves out before being fed would of their own accord go into the box, cats that had been from the first dropped into the box at the top never learned to go in of their own accord. He argued that if a cat had been able to have the idea of being in the box, as a necessary prelude to food, it would have been able to pass from the idea of being dropped in to that of going in itself. This argument, however, is not fully convincing. The experience of being picked up and dropped into a box is very different from that of walking through a door. To the human mind, accustomed to more refined analysis of its experiences, one of these would suggest the other, but we cannot argue that because such a connection is not made in the animal's mind, therefore the latter is incapable of ideas, any more than we could conclude a total absence of ideas from the consciousness of a man to whom a primrose by the river's brim does not suggest thoughts of the moral government of the universe. Moreover, several observers have reported precisely this ability to get the habit of jumping into a box from being dropped in; our rabbits (1035), which were put into a box for safe keeping between experiments, within two days acquired the trick of running to the box and scrambling into it, the whole experience being a prelude to food.

The same comments, precisely, apply to Thorndike's observation that his dogs and cats were not helped to learn a puzzle-box mechanism by being put through the movements. The absence of ability to pass from the experience of being put through a movement to the idea of performing the movement is no proof of incapacity to form ideas; moreover Cole (180) found that the raccoon did learn to work a fastening by being put through the movements. Hunter (479) made a similar observation on the rat, and the method seems to meet with success in the hands of animal trainers.

In general, however, we must admit, the facts point to the

conclusion that ideas are very rare in the animal mind. We can in some cases, however, present positive evidence of their occurrence. One attempt to demonstrate them, that of Cole (180), it is true, seems hardly conclusive. Cole trained raccoons to discriminate between various stimuli. Cards were placed on levers so that by a touch they could be pushed up and down. The animals learned to climb up for food when one of two differently colored cards was shown, and to stay down when the other one appeared; to distinguish in a similar way between a high and a low tone, between a round and a square card, and between a card $6\frac{1}{2} \times 6\frac{1}{2}$ inches and one $4\frac{1}{2} \times 4\frac{1}{2}$ inches square. Of course the action of climbing up was not itself purely instinctive, but had become associated with the food instinct. The raccoons also hit upon the trick of clawing up the cards themselves, and if the one that appeared was the "no-food" card, they would either claw it down again and pull up the other, or proceed at once to pull up the other, leaving the "no-food" one also up. Since the cards were shown successively, Cole concludes that "remembrance of the card just shown was required for a successful response." "Why," he asks, "should the animal put the red card down if it did not fail to correspond with some image he had in mind, and why when he put the green up should he leave it up and go up on the high box for food if the green did not correspond with some image he had in mind?" It seems to the writer that the supposition of an image is unnecessary, except possibly in the experiments requiring discrimination of sizes. It is perfectly possible, as we know from our own experience, to react to one stimulus and not to another without going through a comparison of the two, unless the difference between them is merely one of degree. It might have been possible for a human being to discriminate between the larger and the smaller cards only by calling up a memory image of the card not shown and comparing it with the one before him; it surely would not have been necessary for him to use images in the reactions to colors, forms, and

tones. And if a human being, accustomed to much dependence on memory ideas, could get on without them here, surely a raccoon could. Even in judgments of degree, all laboratory psychologists know that human beings have a strong tendency to make absolute rather than comparative judgments, and use memory ideas but little. Better, though still unsatisfactory, evidence of the use of images is furnished by the following method: "Three levers were placed on the displayer. One, on being raised, displayed white, another orange, another blue. The plan was to display white, orange, and blue consecutively, then to display the same blue three times. I fed the animal if he climbed upon the high box on being shown the series white, orange, blue, and did not feed him after the series blue, blue, blue." That is, the stimulus immediately preceding the reaction was the same in both cases. The difference lay in the foregoing stimuli. The series "white, blue, red, food" and "red, red, red, no food" was also used. The raccoons learned to respond properly, "though," Cole continues, "I never *completely* inhibited the animals' tendency to start up on seeing white or blue, which were precursors of the red which meant food. Thus the animals all anticipated red on seeing its precursors, which in itself seems good evidence of ideation. Many times, however, they turned back after starting at blue or white and looked for the red, then climbed up once more, thus showing that the red was not a neglected element of the situation, but an expected color which they generally waited to see, but sometimes were too eager to wait for." Certain details of the raccoons' behavior are significant. "Each one, on seeing the first red, would drop down from a position with both front paws on the front board to stand on all fours in front of it, and merely glance up at the succeeding reds. As soon as the white appeared, however, the animal would lean up against the front board, claw down the white and blue, but *never the final red.*"

Now Cole thinks that the learning of this trick by the raccoons proved that "the animal *retains* an image of the cards

which just preceded red." The only alternate supposition seems to him to be that they always reacted to the number of the card in the series, which, if the series were irregularly given, would not have been the same in successive trials. To suggest one's own interpretation of animal behavior that one has not seen, in the place of the experimenter's interpretation, requires some temerity, but to the present writer the most natural way of accounting for the raccoon's performances would be the supposition that in the series white, blue, red, for instance, at the end of which they were fed, the occurrence of white threw them into a state of expectancy, of readiness to climb up on the box; this was heightened by the blue, and finally "discharged" into action by the red. During this process they may have had an *anticipatory* image of the blue and of the red, although there is no evidence that they did. But when the red came they did not stop to call up *memory* images of the preceding colors, and decline to act until they had assured themselves that those were blue and white instead of red. Preparedness to act was probably already secured by the actual occurrence of the white card at the beginning of the series. In other words, while images may have been present, they were images with a future, not a past reference. A human being reacting to a series of stimuli in this fashion would but rarely, in case his attention had wandered during the giving of the first two stimuli, have to recall them as memory images before reaction, but he might very likely have anticipatory images of the stimuli to come while waiting for them. These criticisms, which appeared in the first edition of the present work, were later repeated by Gregg and McPheeters (365), who made experiments similar to Cole's.

In favor of the functioning of ideas in monkeys and raccoons is the fact that in learning to open puzzle-boxes, they drop off useless movements with great speed. And monkeys have given clear evidence of inferential imitation. Kinnaman (540) reports that in one of his experiments, where the box

had to be opened by pulling out a plug, a monkey failed to work the mechanism and gave up in despair. Another monkey then came out of the cage, the first one following. Number two went to the box, seized the end of the plug with his teeth, and pulled it out. The box was set again, and monkey number one rushed to it, seized the plug as number two had done, and got the food. She immediately repeated the act eight times. A second and similar observation was made where the mechanism was a lever. Haggerty (377), as the result of long observation and experimenting on the monkeys in the Bronx Zoo, got some excellent instances of inferential imitation, of which one may be quoted. The act to be performed was that of climbing up the side of the cage, thrusting the arm up inside a wooden chute, and pulling a string inside it, as a result of which food came tumbling down. Monkey number 13 was allowed to watch monkey number 4 go through this process four times. "Number 4 was now removed and Number 13 was released in the cage. At first he looked about over the floor for food and then climbed the front wire, stopping on the brace opposite the chute. He leaned over to the chute and while still standing on the brace with his feet, tried to thrust a hand into the bottom of the chute. Failing in this, he ran along the brace . . . and back again to opposite the chute; catching the rung of the chute in his hands he drew himself over to it; finding himself above the end of the chute he tried to let his body down, first on one side and then on the other, until in the most awkward manner he managed to get near enough to the end to thrust a hand up the inside far enough to reach the string. At once he pulled and the food came tumbling down on his chest and to the floor. Dropping to the floor he picked up the food and ate it" (377, pp. 360-361). Such persistence of endeavor to carry out a definite act would certainly in a human being be guided by ideas.

Again, in Hunter's (479) work by the Delayed Reaction Method, the raccoons showed behavior which would seem to indicate the presence of a memory idea. Although they could

not go in the right direction if more than twenty-five seconds had elapsed since the light was turned off, they succeeded within this interval *whether they did or did not change the position of their bodies*. "Each of these animals could react successfully when the wrong orientation was held at the moment of release, and when, so far as the experimenter could detect, no part of the animal's body remained constant during the interval of delay" (p. 43). Thus, after the light was turned off, and they had moved about during the period of delay, when they were released they could move in the direction where they had seen the light. Dogs and cats, which failed to show this type of behavior in Hunter's experiment, did themselves more credit in other investigations. Walton (1026) got a good percentage of correct reactions from dogs, using four compartments and a delay period of one minute, during which the cage containing the dog was turned through 90° , totally disturbing the dog's position in the cage. When two compartments were used, considerably longer delays were possible, and although various distractions such as the sight of meat, and whistles from the operator, were introduced, they produced little effect. Cowan (204) experimented on a cat in the surroundings of its own home. When the experimenter appeared at one door of the room, the cat on going to a certain spot in an adjoining room could get food; when the experimenter appeared at another door, on the same side of the room as the first, no food was to be obtained. After the cat had mastered this problem she was prevented from going for the food during a certain delay period. This reached thirty seconds with the cat maintaining an average of 68% of correct choices; and during the delay there was no constant orientation preserved on the animal's part.

Anthropoid apes are capable of delayed reactions which strongly suggest the use of memory ideas. The chimpanzees studied by Köhler at Teneriffe (553), having watched from a cage the burying of fruit in the sand outside, on being liberated the next morning ran straight to the spot, which had been

smoothed over and presented no visible landmarks; this type of behavior was repeatedly observed. Buytendijk's monkey Sim (144), while seizing a piece of apple thrown in one direction, watched the throwing of three others in different directions. He then ate the first piece, went and got the second, and sat down to eat it before the window. He next took the third, watched a bird in flight, scratched himself, turned around, sought the fourth piece which had fallen under a board, and having eaten it, sat peacefully looking out of the window.

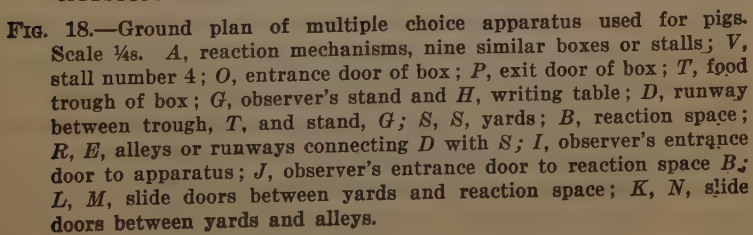
Thus these primates showed good ability to delay their responses when it was a question of finding food: it is interesting to compare with this behavior the fact that Kohts's (556) chimpanzee, engaged in the much less congenial task of matching objects from a sample, failed if more than fifteen seconds elapsed between the showing of the sample and the choice of a similar object from among a number of different ones.¹

Another experimental method which, like the Delayed Reaction Method, has been devised to study the possible functioning of ideas in various animals is the Multiple Choice Method. Its beginnings are to be found in the work of Hamilton (380, 381). As he used it, the essential features were as follows. The animal was placed in a compartment with four exit doors. All of these doors were locked except one, and that one might be any of the four except the door that was open in the previous experiment. The object of the test was to see whether or not the animal approached comprehension of this principle. The subjects were a normal man, a defective man, six boys of varying ages, one defective boy, five monkeys, sixteen dogs, seven cats, and a horse. Only the human subjects reached a stage of learning where they showed by their behavior that they realized the impossibility of opening a door that had been open in the preceding trial. The mon-

¹ A curious type of delayed reaction, which must await further investigation, is reported by Mast (650) of the firefly *Photinus pyralis*. The flash of a female firefly causes the male to move in her direction. The turning of the male occurs *after* the female has flashed.

keys always tried all four doors, but did not often push repeatedly at the same door or persistently neglect a door; this lowest type of behavior was more frequent in the horse. The fact may be noted for future reference that the behavior of the horse in this situation was "stupider" than that of any of the other subjects.

Yerkes (1119) developed the principle of this method and generalized it as follows. (Fig. 18). The animal is offered the choice among a number of compartments. The number can be varied, and their position in space can be varied. Thus, if there are ten compartments in the apparatus, only three of them may be used in a certain experiment, and these three may be situated in the middle or towards either end, so that no associations will be formed with position in space. Or in another experiment five of the compartments, in any part of the series, may be used. The compartments used in a given experiment have their entrance doors open. The problem may be varied in complexity by making the "right" compartment, the one whose entrance gives food, bear different relations to the rest. It may be the first compartment on the left, the first compartment on the right, the second on the left, the second on the right, the middle compartment, and so on. After an animal has proved its ability to learn a simple problem, such as "first on the right," it may be advanced to a more complex one, such as "second on the left." The method has been applied to crows (175), various European song birds (887), rats (137), pigs (1119), monkeys, and apes (1116). The crow mastered the "first at the right" and "first at the left" problems, but failed in five hundred trials to master the "second at the left" problem. Crows having a popular reputation for cleverness, this very moderate achievement renders the performance reported by Sadovinkova (887) for a European siskin the more remarkable. This bird learned the difficult "middle door" problem with a setting of from seven to nine doors, making a score of 24 correct out of 25. One would suspect that it must have been using some extraneous cue, but



the experimenter took care to keep herself, at least, out of sight. The white rat succeeded with the "first at the right," but failed with the "second from the left" problem. The pig distinguished itself by mastering "first at right," "second from left," "alternately first at left and first at right," failing only to grasp the "middle compartment" problem. The two monkeys tested by Yerkes (1116) showed improvement in dealing with the problems "first at left," "second from right," "alternately first at left and first at right," and "middle," but appeared to owe many of their successes to their acquired preferences and aversions for particular compartments. The "alternating" problem proved to be especially easy. Buytendijk's (144) monkey did very badly at multiple choices. An orang-utan, who showed himself in other tests the most intelligent of Yerkes's subjects, failed to improve in solving the problems of the Multiple Choice Method. His wrong choices were so persistent, and so independent of the usual tendency to drop off useless movements, that Yerkes concluded him to be really acting on the basis of *wrong ideas* as to the correct solution of the problem. It is clear that a human being who had formed an incorrect theory as to the proper way to work out a problem would take longer to solve it than an animal who learned merely by the dropping off of useless movements, provided that the animal could solve it at all.

We may now examine the relation of the Multiple Choice Method to the question of the existence of memory ideas in animals. In the first place, if the "right" compartment always occupied the same position in space, clearly an animal might learn to go to it without the use of memory ideas. Kinæsthetic memory, the formation of a habit of turning in a certain direction, would suffice. Next, if the correct compartment is not always in the same absolute position in space, but is always the furthest to the right or left of all the compartments used in the experiment, the learning is still easy. The animal has only to combine the habit of turning to the right or left with the observation as to what compartments have their entrance

doors raised: a compartment with closed doors offers no stimulus. Thirdly, even the problem "second from the left," or right, might, it would appear, be solved without the use of a memory idea. The learning need involve only (a) the habit of turning to the left or right, and (b) the habit of reacting negatively to the open door furthest in this direction. The natural result of such a combined habit would be entering the door *next* to the end door. The problem of entering always the middle door of those open brings us closer to the use of memory ideas. An animal that had solved this problem would, on being confronted with the series of doors, find itself in an attitude representing a balance between the impulse of turning to the right and that of turning to the left. "Middleness" means a slight impulse to turn in one direction, offset by an equal impulse to turn in the other direction. Now the characteristic by which this situation differs from the other situations, involved in the simpler problems, is that the animal must not move at once, but must wait and assume the balanced attitude before moving. In the case of the other problems, he can start off immediately. Here an attitude must be revived before there is any actual movement. Just as in the Delayed Reaction Method success means, if the animal moves during the interval of delay, that it is able to revive an inner attitude which means motion towards the light, so here success means ability to revive an inner attitude which means movement towards the middle, a balance between right and left movements.

Further, what is the difference between reviving such a motor attitude at the sight of a stimulus, and making an ordinary response to a stimulus, such as any animal may learn? The difference is that in the latter case an actual, visible movement is made, while in the former case the movement is internally anticipated and not externally visible. Such an internally anticipated movement is probably always present when in the human consciousness we have a memory idea: when I recall a mental image of an object such as a fork,

I "internally anticipate" the movements of handling the fork. Whether the converse of this proposition is also true, and we invariably have memory ideas whenever we internally anticipate movements, is highly doubtful, but at least it may safely be said that an animal which gives evidence of being able to anticipate its own movements has the possibility of memory ideas in its consciousness. (For reasons which have been elsewhere stated (1033), the present writer is inclined to think that this internal anticipation of movements means actual slight contractions of the muscles involved in performing the movements). Whenever, then, as in the case of success in the Delayed Reaction Method where the bodily position is varied, in that of inferential imitation, and in that of choosing always the middle stimulus, the behavior seems to demand that the movements shall be anticipated by the animal which performs them, we have evidence in favor of the memory idea.

Closely related to the problems presented by the Delayed Reaction and Multiple Choice Methods is the so-called Alternation Problem. As presented by Carr (160) to white rats, it required that an animal should learn to push a door on the right in one experiment and a door on the left in the next experiment, through a series of trials, with no other cue except that of rightness and leftness. Eight rats mastered the alternation in an average of 412 trials, and the interval between trials could be increased to one minute without affecting accuracy, though beyond this limit there was a falling off. What about the motor attitude during delay? A series was made in which the rats were allowed to run about freely on a table during the delay period. This diminished the number of correct choices for certain individuals, but left it still considerable: some individuals, Carr concludes, depend more on motor attitudes and others on "the sensory consequences of the previous act." Incidentally, it may be noted that those rats which were more dependent on constant motor attitudes learned more quickly. In a later study (161), Carr required

the rats to run around a passage to the right and then around one to the left: his conclusion is that they can form an association between two such runs separated by a time interval as long as 35", provided that this interval is filled with "some rather constant type of activity, such as eating." Is there revival of a memory idea here, or of an incipient motor attitude? There certainly would be in a human being. Carr, however, thinks a direct connection between the sensory consequences of one movement and the full arousal of the next may occur in spite of the temporal gap, because practice has set the motor centers in so high a state of readiness.

In one investigation (15) rats were confronted by four compartments, the lights over three of which were flashed on successively. In one series the rat was to go to that compartment whose light had been flashed on first; other rats were required to learn that the compartment illuminated second was the correct one; still others to choose that illuminated third. With sympathy for the harassed animals one reads that they totally failed, and had recourse to position habits!

Incidental features of behavior sometimes suggest the presence of memory ideas; such as for example very sudden alterations in a course of action, or manifestations of "surprise." Thus Buytendijk's monkey (144) observing that desirable articles such as spiders or apples had been placed under inverted flower-pots, had the habit of turning the pots right side up: in one case the experimenter put the apple under a small flower-pot over which he placed a larger one. Sim "reversed the large pot with an energetic movement of his hand. Then there was a pause (astonishment?), after which the animal examined the large reversed pot attentively, then regarded the small one, reversed the latter, took the apple and returned to his post by the window." Buytendijk contrasts this manifestation of astonishment with that shown by a dog when a box which he is sniffing suddenly opens: in the dog's case there is fright at something unexpected, in the monkey's surprise at the non-appearance of something defi-

nitely expected. There is of course a margin of error possible in such interpretations.¹

§ 80. "Insight"

The German psychologist Köhler is one of the leaders of the "configurationist" school, which insists that in all conscious experience the important thing is the total situation. In accordance with this view, instead of saying that first one stimulus and then another one is reacted to, we should say that reaction is made first to the total situation with one part of it emphasized, and then to the total situation with another part emphasized: it is thus the pattern that has changed. From this point of view Köhler has been interested in the solution of problems by animals (551, 553), especially their solution not by accident but by what he calls insight. The external marks of difference between a solution by accident and one by insight are (a) that the achievement by insight forms one single continuous occurrence, while "a successful chance solution consists of an agglomeration of separate movements"; and (b) that the moment when a solution by insight occurs in the animal's mind is often marked "by a kind of jerk," a sudden pause followed by a complete change of behavior (553, p. 17). Thus, to amplify (a), if several successive acts are necessary to attain food, by accidental solution Köhler would mean that each act is independently learned by a chance success, and connected with the next act by mere external association. As we shall presently see, it may well be doubted if such a type of learning occurs in any animal: even where the requisite movements are accidentally discovered, they are from the beginning unified by the presence of the drive or motive to solution. Many cases of learning by insight are described by Köhler, espe-

¹ To lack of the power of recalling memory ideas in the intervals between learning periods Tsai (1982) is inclined to ascribe the fact that for maze running by rats Ebbinghaus's law that forgetting occurs more rapidly at first than later does not hold, though it does for maze tracing by humans.

cially in the chimpanzees he observed at Teneriffe. They comprise instances where a roundabout path is suddenly taken by an animal which can reach its objective in no other way; where objects such as sticks or blankets are used to draw in the otherwise unattainable banana, or boxes piled one on another to reach it; where obstacles in the path to the objective are suddenly removed by the animal, and where tools are constructed, the parts of a jointed rod being fitted together. Similar behavior in anthropoid apes is described by Yerkes (1116).

It seems plausible to describe the change which occurs in an animal's conscious state when such a flash of insight, such a sudden solution of his problem, takes place, as an alteration in its total pattern: certain objects which were formerly in the background now stand out against the background. The ape's consciousness at one moment is dominated by the unattainable banana; at the next moment the stick lying on the ground assumes prominence along with the banana. But it seems equally true that insight requires in many cases the memory idea, and in many others at least that incipient revival of movements which we have regarded as the basis of a memory idea. Take a very simple case of insight: a dog tries to get the food on the other side of the bars, and then suddenly turns through 180° and runs around a corner, reaching the food by an indirect path. He would not act in this way unless he suddenly remembered, either that a roundabout path existed in this particular case, or at least that on former occasions roundabout paths had led to goals. His first discovery of this fact would of course have been accidental. The infant ape may very likely have learned by accident that objects can be reached by poking sticks at them: his sudden insight in the present situation would involve recalling such experiences, not necessarily of course in complete detail as memory images. Lindworsky (583) and Bühler (133) suggest that the association of fruit and branches must be frequent in the natural life of arboreal

animals, and Buytendijk (144) explains the failure of his monkey to draw in food by means of a stick, through the fact that monkeys are light enough to run out to the end of branches and get food, while apes have to haul the branches in. Köhler (553, p. 213) objects to Bühler's memory-idea theory, pointing out that a wild ape would get food by pulling in branches or breaking them off, whereas his apes used the stick to draw in the food. This objection will hold against the supposition that recall of memory ideas is the sole and sufficient explanation of "insight": we are here merely pointing out that such recall, more or less (often less) definite and detailed, is involved in insight. Köhler himself mentions several cases where obvious use is made of a memory idea; as for example when the chimpanzee Sultan, after vainly trying to get a tool that would reach a suspended bit of food, "quite abruptly and without visible external cause" ceased his efforts, "remained for a moment motionless, sprang to the ground," ran around a corner and returned with a box which he had previously seen in the position where he now sought it, and upon which he now proceeded to climb for the food (553, p. 54). In most of the cases of insight, however, the solution occurs not by introducing an object absent at the outset, but by the emergence into the "focus of attention" of an object already present but disregarded. Our theory would suggest that this emergence happens because the sight of the relevant objects sets off slight recurrences of the movements by which in past experience they have been reacted to; that is, slight anticipatory movements such as would, if the objects were not present, revive memory ideas of them.

§ 81. *Conditions Favoring the Development of Memory Ideas*

An important condition of an animal's ability to anticipate its movements, to "know beforehand" what it is going to do, is obviously the ability to keep from actually reacting on the instant when the stimulus acts. To recall a memory idea, to

anticipate by slight and invisible movements the response one is going to make, implies waiting a brief interval at least before making it in full. Now the development of sense-organs which can receive stimuli coming from a distance is an absolutely necessary prerequisite for the safety of delaying reaction. An important difference exists between the stimuli from objects directly in contact with an organism's body, such as in our own experience give rise to touch, temperature, pain and taste sensations, and those which proceed from objects at a distance, such as light, sound, and odors. This difference consists in the fact that the former have a more direct and instant effect upon the organism's welfare, and in consequence demand more rapid reaction than the latter. A stimulus in immediate contact with an animal's body may have a harmful or beneficial influence at the moment of its impact; it may be food to be seized or an enemy to be escaped, and the seizing or escaping must be done on the instant; on the other hand, if an animal possesses the power, belonging in an increasing degree to animals as we go up the scale, of reacting to influences proceeding from objects still at a distance, it may safely delay its reaction when the stimulus is given. The danger is not so imminent, the food is not yet within reach; the full motor response to stimulation may be suspended for a short interval without imperiling the life interests of the animal. Thus one condition for the development and use of memory ideas is *the evolution of sense-organs for the reception of stimuli at a distance*. This idea was first suggested by the writer in 1904 (1032); a similar conception, developed from the neurological standpoint, appears in Sherrington's "The Integrative Action of the Nervous System" (928, pp. 324 ff.). Sherrington proposes the term "distance receptors" for those receptive organs "which react to objects at a distance," and declares that "the distance receptors contribute most to the uprearing of the cerebrum." The most important significance of the power to act in response to distant objects Sherrington finds to be that it

allows an interval for preparatory adjustment, "for preparatory reactive steps which can go far to influence the success of attempts either to obtain actual contact or to avoid actual contact with the object." That these preparatory steps may also involve the germ of the memory image is clearly suggested by Sherrington. "We may suppose," he says, "that in the time run through by a course of action focussed upon a final consummatory event, opportunity is given for instinct, with its germ of memory, however rudimentary, and its germ of anticipation, however slight, to evolve under selection that mental extension of the present backward into the past and forward into the future which in the highest animals forms the prerogative of more developed mind. Nothing, it would seem, could better insure the course of action taken in that interval being the right one than memory and anticipatory forecast" (p. 332).

Secondly, if memory ideas depend on the anticipation of movements, during the delay between stimulus and full response, an important condition of their variety and free use is the *ability of the animal to perform a great variety of movements, and especially of movements other than those of locomotion*. Locomotion gets an animal into difficulties and rescues it; movements of locomotion are of the first practical importance. But they have not a great deal of variety. It is not merely a coincidence that the best evidences of memory ideas should appear in animals which like the raccoon and the monkey are dexterous, able to use their paws for movements more complex and refined than those of locomotion. The supreme development of ideas comes in the mind of the animal which has not merely hands, but vocal organs, so that an infinite variety of delicate and complicated movements can be anticipated, and can form the basis of memory ideas.

Thirdly, one of the conditions of the anticipation of a movement appears to be *attention* to it when it is originally performed. In order to remember a movement, we must have paid attention to the sensations which its performance

occasions, to the way it feels to make the movement. And one condition for attention to the way a movement feels is being comparatively safe from external dangers when the movement is made. An animal under ordinary conditions of wild life has very little attention to spare for his own movements. It would thus seem as though one requirement which must be fulfilled if anticipated movements are to play an important part in a creature's experience were that the animal should, for a time at least, be set free from the pressure of the practical hand-to-hand struggle for the means of existence, and thus enabled in safety to attend to its own movement sensations. Animal play, at first thought, offers an instance of such liberation from practical necessities. But as Groos has shown, animal play is not so unpractical as it looks (367). It is simply the exercise of the same instincts upon which in other circumstances the animal's welfare depends. The attention is absorbed in external objects quite as much in play as in the actual chase or warfare. The kitten watches the string, for which she has no practical use, as intently as she watches the bird for which she does have a practical use; the dogs rolling over and over each other are nearly as absorbed in each other's movements as if they were in deadly combat.

That relief from practical necessity which will serve the purpose we are considering is to be found not in play, but in infancy. If a creature spends the period during which its nervous system is undergoing most rapid development in a state of complete shelter and protection from external danger, with all its vital needs supplied, then the nervous energy which under other conditions would be expended in the processes underlying attention to external stimuli is free to be so devoted that attention will be directed toward the creature's inner experiences. The human baby, while he may be interested in lights and sounds, in external impressions, does not need to be alert and watchful lest he miss his dinner or be dined on himself; his attention is free to be ex-

pended on his own movement experiences as well as on anything else. That young children do go through a stage of intense interest in the sensations resulting from their own movements is a fact made clear from many observations. The curious period of "self-imitation" in the child when it repeats for an indefinite period the same movement or sound, over and over again (23), is very likely a period of vivid attention to movement sensations.

That the prolonged period of human infancy is of advantage to the intellectual life of man because it means plasticity, the absence of fixed instincts that would take the place of acquisition by individual experience, was first pointed out by Fiske (303). But quite as important is the fact that in prolonged infancy we have the opportunity for acquiring the habit of that attention to our own movements which is the prerequisite for anticipated movements. There are, as we have seen, various ways of learning by experience—slow ways that do not involve ideas, and the rapid way that does. The great advantage of man over most of the lower animals is not so much in the fact as in the method of his learning. One of the most vital meanings of the long period of helplessness and dependence constituting human infancy lies in the fact that by relieving from the necessity of attending exclusively to external objects, it renders possible attention to the sensations resulting from movement; and thus, by supplying an essential condition for the anticipated movements, it opens the way for the control of movement through ideas.

§ 82. *Some Alleged Instances of Remarkable Mental Powers in Animals*

All of the experimental evidence which we have examined indicates that even in the cleverest animals intellectual ability falls far short of that demonstrated by rather dull human beings. But a few years ago in Germany the hypothesis was advanced that the minds of such animals as horses and

dogs are really quite on a par with those of human beings; their apparent deficiencies being due to the fact that we have never learned how to educate and communicate with animals. In 1901 a Berlin gentleman, Herr von Osten, began training a five-year old horse named Hans to answer arithmetical questions by tapping with his hoof on the ground. Taps with the right hoof meant units, taps with the left hoof meant tens. Later, an alphabetic system was constructed on a numerical chart: the letter *a*, for example, being found in the vertical column numbered 3 and the horizontal column numbered 2, tapping three times with the left hoof and twice with the right meant *a*. Thus Hans was trained to answer questions other than those concerned with numbers. He showed ability to do so with seeming intelligence, and to work arithmetical problems. He was examined successively by two commissions, and a psychologist on the second commission, Pfungst, apparently solved the mystery of Hans's behavior by showing that the person who put the questions to the horse made unintentionally a slight movement of the head when the proper number of taps had been given, and that when such movements were intentionally made, the horse responded to them. So the matter rested, with the simple solution that the horse had, instead of really thinking, merely reacted to involuntary signals. After the death of Herr von Osten, Hans came into the possession of Herr Krall, a business man of Elberfeld, who was not satisfied with Pfungst's explanation, and besides continuing the education of Hans, trained several more horses, the most gifted of which were two Arabians named Muhammed and Zarif. In two weeks Muhammed learned to add and to subtract; he passed in three days from multiplication and division to the use of fractions; he acquired remarkable skill in the extraction of square and cube roots, and finally he as well as his fellow pupil began to offer original observations. These performances occurred even when the horses were prevented from seeing any one. Much the same sort of phenomena are reported

in the case of Rolf, the Mannheim dog. The more recent reports of the Elberfeld horses are less enthusiastic, and even claim fraud, although not on the part of Herr Krall, whose disinterestedness seems accepted. It is impossible to determine just what cues are responded to by these animals in their performances, but aside from all the negative weight of the evidence obtained under exact experimental conditions on other animals (it will be recalled that the horse was the stupidest of all Hamilton's subjects), certain indications point clearly away from the possibility that the horses are really mathematical geniuses. (1) They learn too quickly to allow of their understanding. A gifted human being could not acquire so fast a real apprehension of mathematical relationships. (2) They take no longer for hard problems than for easy ones. (3) They begin tapping without even glancing at the problem written on the board. (4) The character of the mistakes they make is not that of the mistakes of a real calculator: very common errors are reversals of the figures, thus 27 for 72, or errors of one unit, as 21 instead of 22. These are errors which might easily be made if the two forefeet were confused in the tapping, or if the tapping stopped a little too soon or not quite soon enough. They are not real arithmetical errors, such as forgetting to carry a figure over from one column to another, for instance. (4) No really satisfactory results have been reported when no one present knew the correct answer. On the whole, the phenomena do not present themselves with such authority as to compel a revision of our whole conception of the animal mind (171, 172, 270, 376, 516, 633, 634, 679, 711, 792, 891).

§ 83. *Certain General Conditions of Learning*

Before attempting to draw conclusions on the general theory of learning, we have to discuss certain influences affecting it which have not been brought into clear relief by the facts so far considered.

(1) To begin with less important ones, the *age* of an animal influences its ability to learn. Watson (1046) compared the capacity of young white rats with that of mature animals in the learning of puzzle-box and maze habits. He was especially interested in testing Flechsig's theory that learning depends upon the presence of medullated fibres in the central nervous system. The theory was unconfirmed, for such medullation is highly imperfect in the rat at twenty-four days of age, yet at this age Watson's rats learned a labyrinth more quickly than did the adults. The rat belongs to the class of animals that are born unable to care for themselves, and before those observed by Watson had reached the age of twelve days, they were unable to find their way by a simple maze path back to the mother. The superiority of young rats over adults in learning a maze path is apparently due to their greater activity; they make more useless movements, and in solving a puzzle box they are at a disadvantage as compared with their elders.

Allen's (6) work on the guinea pig was intended for comparison with Watson's study, because the guinea pig comes into the world, not helpless like the baby rat, but well equipped on both the sensory and motor sides. In the labyrinth tests the mother was put at the end of the maze, and the sight and smell of her were supposed to serve as the stimulus to activity. Before the young animals reached the age of two days they did not succeed in learning a comparatively simple path, but at that age they did learn it, and proved the fact when the wire netting box in which they were placed was turned about, by pushing at the place where the opening had been. At three days they learned a more complex maze, and appeared to possess the learning capacity of adults.

Yerkes (1113) found that the dancing mouse at one month old learns a black-white discrimination faster than an older mouse. From one to seven months of age there is a decrease in learning speed; from seven to ten months, an increase. The power to discriminate appears to be better in younger mice;

the power to associate, better in older ones. Thus the superiority of the younger animals is rather in speed of sense perception and movement than in real learning ability.

Hubbert (473) has confirmed the statement that young rats learn the maze more rapidly than older ones. Moreover, she finds that in the younger animals, the most rapid stage of the learning occurs at an earlier point.

(2) The *sex* of the learner may have some effect on the learning, although no very definite differences have thus far appeared. Yerkes (1113a) reports that young male dancing mice learn faster than females, and that females from four to ten months of age learn faster than males. Hubbert (473) states that except in the cases of very young and very old rats, males learn more readily than females; the absolute time of running the maze is however shorter for females.

(3) The *differences in individual ability* among animals are marked. We are inclined to think of all the animals of a certain species, especially if it be a species far removed from man, as equally gifted, but it is quite possible that among ants and earthworms there are geniuses and dunces. Turner (994, 995) reports striking individual variations in the behavior of cockroaches learning a maze; two of the rats tested by Small (933) with puzzle boxes never learned to get into the boxes, but merely profited by the activity of their more gifted companions. Wodsdalek (1084) gives a delightful account of a specially talented Mayfly. Practically every experimenter reports similar individual variations.

Katz and Toll (533) have made a series of character studies of individual hens that is both important and entertaining; besides differences in intellectual ability the hens show variations in excitability, timidity, and greed.

(4) *Differences in the sensory endowment* of animal phyla, genera, and species of course influence their learning processes. Szymanski is especially interested in these differences. He writes of tactile, visual, and osmic animals (956, 958);

also of motor and sensory types, the dog being more motor, for example, that is, tending to depend on kinæsthetic clues; the cat more sensory, in particular, more visual (961). This point he illustrated by experiments showing that when dogs have been trained to go to a food-box in plain sight, if it is put in another, but still visible, location, they follow their motor habit and seek it in the old place: whereas cats in similar conditions correct their course by vision much sooner. Young animals, he says, and animals in periods of activity, are more motor. Less rigorous experimental conditions favor a more sensory type. Revesz (858, 860) has shown the extremely visual type of the fowl, so marked that the birds will not peck at grain in the dark.

(5) The *distribution of practice* affects the speed of the learning; Yerkes (1113) found that the dancing mouse learned a white-black discrimination in a smaller total number of trials, the smaller the number of trials per day. Ulrich (1003) has shown that the white rat learns a puzzle-box habit or a maze habit in fewer trials if one trial is given a day, than are required if either three or five trials are given a day. Apparently even better results were secured by one trial every third day. The same principle appeared to hold when several problems were being learned at once. This principle, known as that of distributed repetitions, has long been recognized in human memorizing, which is always more economically secured if intervals of time are allowed to elapse between repetitions. The reason is as yet undetermined. It is clear that the interval between repetitions must not be so great that forgetting occurs. One theory to explain why, within this limit, longer intervals are more favorable than shorter ones supposes that a process of fixation of the impression occurs in the nervous system, which is interfered with if a new impression follows too quickly. Warden (1029) thinks this one of the factors involved, but Lashley (577) does not incline towards it, because there is no other evidence for the occurrence of such a gradual fixation process. An-

other hypothesis is that an interval allows time for certain erroneous tendencies to drop out; the assumption being that their rate of dropping out would be faster than that of the correct movements. Lashley, testing fifty rats in the circular maze, confirms the influence of this factor by finding that a higher percentage of repetition of errors occurred when there was no interval between trials (576). Lashley points out also that short intervals, involving frequent removals of the animals from the food-box, tend to accumulate the disturbing effects of this proceeding upon the rats. Still another suggestion to account for the law of distributed repetitions as seen in both human and animal learning was made by the present writer (1033, p. 122). We know from the occurrence of the memory after-image in our own experience that shortly after a movement has been performed it is in a state of readiness to be performed again, a condition that rapidly diminishes with lapse of time since the original performance. Hence if a second performance is made to follow the original one too closely, its normal effectiveness in reducing the resistance at synapses will be lessened by the fact that it finds them already low. Warden (1029) is inclined to accept this as one factor. From his own experiments, which were complicated by the fact that he studied the influence of intervals between groups of repetitions instead of between single repetitions, he concludes that the main advantages of lapse of time between performances are better fixation, and the dropping out of weaker interfering tendencies.

(6) The learning of one habit may influence the later acquisition of other habits. This influence may be in the direction of facilitation, or *transfer of training*; or it may consist of *interference* with the formation of the new habit. It seems *a priori* clear that facilitations will occur when the old and the new habit do not involve incompatible reactions, such, for instance, as movement in two opposite directions with reference to the same stimulus; and that interference will occur when the two habits are incompatible.

Transfer often occurs in maze experiments. Thus Yerkes (1113) reports that dancing mice which have learned one maze learn another one more readily than those which have had no previous training. Wiltbank (1078) found that if two mazes were completely learned, one after the other, there was a saving in time, number of trials, and errors, in learning the second maze. When the first maze was only partially learned, even two trials in it served to shorten the time of learning the second one; but it required sixteen trials in the first maze to shorten time, number of trials, and errors. When the first maze was partially learned, the second one completely learned, and the learning of the first one then resumed, transfer occurred if the partial learning had consisted of from two to eight trials, but if it had gone as far as sixteen trials, interference occurred: that is, the continued learning of Maze I was hindered by the interpolated complete learning of Maze II. This is unexplained: why, if I does not interfere with II, should II interfere with I? In human memorizing it has been found that a new habit is less likely to interfere with an old one than an old one with a new one. Dashiell (231) studied the effect on the process of maze learning of the following kinds of preliminary training: getting food from the maze food-box by pushing open the door; passing through a short crooked passage before getting food from the box; running another, simple maze; running twenty-five different mazes on twenty-five successive days, one trial a day. The last two types of training were beneficial: the rats did not hesitate so much on their initial trials as did those trained by either of the first two methods.

It is clear that in maze learning the occurrence of incompatible responses would be rare. An animal transferred from one maze to another will seldom be able to try its old habit, unless the two mazes are the reverse of each other. Hence interference would be at a minimum, but why should actual assistance occur? Probably because the general maze situation has become familiar to the animal, and associated

with food: he has learned to press onward and to suppress the tendency to explore blind alleys.

Discrimination experiments, on the other hand, usually involve *interference* rather than transfer. In our (1036) experiments on the fish, after training it to bite at red forceps rather than green ones, we undertook to reverse the habit. At the first trial with food in the green fork, the fish ignored it and bit fourteen times at the empty red fork close beside it. Hunter and Yarbrough (488) found interference when auditory stimuli were used to establish habits of turning right or left. Pearce (772), after training rats to run left for light and right for darkness, attempted to reverse the habit; the result was almost complete blocking of the new habit. Hunter (486), with the same pair of habits, reports that if the first habit was completely learned, the formation of the second one took about twice as long as if it had been learned first. If the first habit had been half learned, that is, given half the number of repetitions required for complete learning, the interference with the formation of the second habit was about half as great. In all these experiments, of course, the movements involved in the first habit are directly incompatible with those involved in the second. There was probably also incompatibility in the puzzle-box habits with which Yoakum (1125) found interference in the case of squirrels. Hunter (478) reports interference between maze habits in pigeons: it is possible, since birds are so much more visual than motor animals, that confusion arose from the visual surroundings in this case. Szymanski (960) found absence of transference under the following conditions: rats were trained to enter one compartment by creeping under a partition, rather than another by creeping over: they were then set to learn a maze where the first choice was that of turning right and creeping under, in place of turning left and creeping over a partition. They showed no effect of their previous training. They could not generalize, Szymanski

says; at least, we may say, the alteration of the other conditions must have operated as a distraction.

Closely related to these experiments are those where the new discrimination habit involves different stimuli from the first one, but stimuli which have the same relation to each other as in the first case. Thus in our experiments on color discrimination in rabbits (1035), an animal learned to choose red rather than light grey, because the red looked darker than the grey; when the same grey was used with white, the rabbit chose it in a high percentage of the trials. There is here direct transfer rather than interference. Such cases have been considered in connection with the problem of perception (pp. 241 ff.). Here the point that concerns us is that the two stimulus situations are probably not distinguished by the animal: both consist in the presentation of a difference in brightness, and the fact that the absolute brightness has changed is unobserved. We may sum up the possibilities in regard to interference in the case of discrimination experiments, as follows: When one stimulus is substituted for another, (a), the two may not be distinguished by the animal. In this case of course there can be no interference, as the same reaction is given to both. (b) The second stimulus is associated with a response not incompatible with that belonging to the first, although differing from it: in this case there will be no interference. (c) The two stimuli are associated with incompatible reactions: interference results.

(7) The most important of all conditions governing learning is the *motive or drive*. In the first place, we may compare punishment and reward, harm and benefit, as influences in learning. Punishment, unless it is so severe that it attaches itself to the whole learning situation, appears to produce more rapid learning than does reward. Punishment and reward combined give, probably, better results than either alone (454). Further, a movement resulting in harm, which is therefore supplanted by the negative response of withdrawal, is more completely eliminated than one that is merely

useless and is supplanted simply by a state of rest. Evidence of this was obtained by Bogardus and Henke (75) in experiments where, after rats had learned a maze, the path was altered, certain passages being closed and others opened. The rats found it decidedly harder to learn to enter former *cul-de-sacs* than to take those turnings which had been omitted merely because they were a longer way around than the true path. The checking movement produced by running against the end of a *cul-de-sac*, like the withdrawing movement from punishment, was rapidly substituted for the tendency to enter. Kuo (567) used a multiple choice apparatus with rats, offering a choice between an electric shock, confinement, a longer path, and a shorter path to the food box, and found that the electric shock compartment was avoided sooner than the others.

Next, considering punishment, we may discuss the effect of its strength. Obviously this depends not only on the amount of energy in the stimulus, but on the sensitiveness of the punished animal. Yerkes was the first experimenter to employ the electric shock as a means of training animals. He used it on the frog (1098), which he was trying to educate to make a turning to the left rather than to the right: the frog showed a discouraging tendency to sit motionless for long periods of time, and so Yerkes placed electric wires on the floor, to induce by a mild shock greater activity. In his work on the dancing mouse (1113), he substituted the giving of electric punishments in the case of wrong choices, for the older method of rewarding an animal's right choices, and one of the advantages claimed for this method was that it seems to allow an exact measurement of the strength of the stimulus, whereas a reward, such as food, varies in strength with the animal's physiological condition. But the effect of an electric shock too varies with the temporary physiological state of the animal, and with its general individual sensibility. Yerkes (1120) carried out some interesting experiments on the relation of the strength of the punishment to the difficulty

of the discrimination required of the animal. A superficial consideration of the situation might assume that if one wants to teach an animal a difficult discrimination, such as that between two slightly different shades of grey, one ought to supply a stronger punishment stimulus than would be necessary to teach it an easy discrimination, such as that between black and white. The results with the dancing mouse showed on the contrary that weaker punishments were more effective in the learning of hard discriminations; stronger punishments in that of easy discriminations. The same rule was found by Dodson to hold for cats (252); the hardest discriminations were acquired by kittens in 82.5 trials with a moderate stimulus, but 107.5 trials were required on the average with a strong stimulus. Indications of a similar relation were found by Cole (182) in the learning of chicks. Dodson (253) reports that with rats the effectiveness of electric shocks reached its maximum at a fairly low intensity of current. The fact seems to be, as we have seen, that very strong punishment produces withdrawing reactions which attach to the whole apparatus as stimuli, and also probably general disturbances of terror and excitement.

We may turn now to the consideration of rewards. In order that a stimulus shall constitute a reward, clearly two things are necessary: a state of desire on the part of the animal, and the satisfaction of that desire by the stimulus. Food is not a reward to a sated animal. In the first place, it seems obvious, and can also be experimentally shown, that an animal will not learn without reward, except through punishment. Obvious, and yet if Watson's theory that learning occurs through the influence merely of frequency and recency were true, reward would be superfluous. Szymanski (959) has shown that rats will not learn a maze if there is no food in the middle; and if they have previously learned it, they will not run it well if they have just been fed (956). Dashiell (232) has ingeniously illustrated the effect of hunger on the tendency to general activity by using a floor marked

off into squares, and noting how many squares are traversed by a given animal in a given time. The number was decidedly greater for hungry than for fed rats, although no food was present. The presence of a desire or drive produces general activity in the animal, which is of course an essential condition for learning new movements. But although activity is an essential condition, general activity is not enough: there must be a definite forward drive. Szymanski (957) observed that his white rats were especially active during the evening hours and sluggish between seven and ten A. M.: he compared their ability to learn a maze during a period of activity and during a period of rest, and found no important differences. Liddell (582) likewise found no relation between speed of maze-learning in lambs, and their periods of spontaneous activity, measured by a pedometer.

The present writer (1034) has compared the effectiveness of speed of running directed by hunger, and speed of running determined only by general activity, as influencing maze learning in white mice. The rate at which the mice ran, that is, the total time of running divided by the length of the course traversed, errors and all, was recorded for each mouse day by day, and also the length of time each mouse ate on reaching the center. Certain mice ran faster, the longer they ate the end of their course; others showed no such correlation. It may be concluded that the speed of the first group was determined by hunger mainly, and that of the second group by the impulse to general activity mainly. It further appeared that in the case of the first group, the runs made at greatest speed were accompanied by fewest errors, which was not the case with the second group: hence speed is favorable to learning only when it is hunger-determined, or at least determined by some forward drive. The influence of the forward drive, of course, begins only when the reward has actually been found, or can be detected from a distance.

Various experiments have been made to compare the effectiveness of the same drive in different strengths. Hunger is

the forward drive whose intensity can be best controlled experimentally: the obvious method is to keep the animal without food for periods of different length. The control is imperfect, for physiological changes from internal causes may complicate the situation. A human being deprived of food for six hours feels very different degrees of hunger when he is in a normal state and when he has a fever. This type of control was used by Dodson (253), who reports that the effectiveness of hunger on rats increases with increasing intervals since feeding, up to forty-eight hours, after which it rapidly decreases; and by Szymanski (956), who finds a twenty-two hour hunger much more favorable for maze-running in rats than satiety, and somewhat more favorable than a five-hour hunger. The indications are that a very intense drive, like a very strong punishment, is unfavorable to learning, because of some general disturbance which it sets up. Carr (157) varied the amount of hunger roughly by varying the length of time during which the rats were permitted to eat: "heavy feeding" greatly increased the error score. Simmons (930) compared two kinds of food, sunflower seed and bread-and-milk, as incentives to hunger in rats: the latter produced quicker learning, probably because of its stronger odor and greater familiarity. A source of error in her work and that of other investigators is the possibility that the groups of animals compared may have had different degrees of native learning ability.

I have tried measuring hunger, as has just been said, by the length of time the animal eats on reaching food. Any attempt to compare the degrees of hunger felt by different individual animals under given conditions, however, suffers from error, because the physiological constitution of two individuals may differ so that deprivation of food for a given time may produce different degrees of hunger in them; and further, the extreme degree of hunger, capable of acting as the most intense drive, in one animal may produce an amount of eating equal to what would indicate only mild hunger

in another individual. The only safe comparisons are between the manifestations of hunger in the same individual at different times.

Different drives have been compared with one another. Tsai (1983) offered male rats a choice between food in one direction and a female in heat in the other: food was chosen 77% of the time. The rats had not been fed for twenty-four hours. Simmons (1930), on the other hand, found the sex drive on the whole stronger than hunger, though variable, and delaying somewhat the initial trials, probably because of the general excitement it produces. Moss (1978) ingeniously pitted different drives against one another by making it necessary for a rat to cross a brass plate in order to satisfy a drive, and measuring what strength of electric charge in the plate would inhibit the animal from doing so. A 72-hour hunger proved stronger than the sex drive. The maternal drive seems to be highly variable in strength. When their three-days-old litters were in the centre of the maze, two female rats out of three paid no attention; the third learned the maze (1959). Six out of twelve rat mothers displayed similar indifference in Simmons's experiments (1930). Moss (1978) finds the sex motive stronger than the maternal one. The motive of return to the home cage was found more effective than that of escape from the maze (1930). The one motive effective for experimental purposes in the case of Kohts's (1956) chimpanzee was the desire to get back to his play.

An interesting idea of Szymanski's (1955) was that of allowing animals to choose their own time for learning; to act on the spontaneous arousal of a drive. This he accomplished, using white mice as subjects, by putting a food dish on a raised platform, reached by bridges, either one of which could be arranged to make an electric record and give an electric shock when stepped on. This apparatus was left permanently in the dwelling cage, and would automatically record how often a mouse visited the food-table, and by what bridge, the one involving punishment or the other. Soon

after the beginning of the experiment, after from one to four contacts with the "shock" bridge, a mouse would reach the food dish; it would then for several of its spontaneous eating periods avoid the shock bridge; then try it again; then have another series of eating periods without touching the bridge, and so on for twenty days. Then, more or less suddenly, the shock bridge would cease to be visited in up to one hundred successive eating periods. This, says the experimenter, represents the period of fixing the habit; and he points out that the occasional breaks in its previous course are of biological value, for seldom under natural conditions would an animal always find food in the same place.

General physiological conditions other than drives, it is unnecessary to state, will affect learning: thus either too little or too much thyroid substance will abolish both the effects of learning and the capacity to learn (865).

§ 84. *The General Theory of Learning*

As we survey the various types of true learning, one phenomenon seems always to be involved. It is that of readiness on the part of a motor centre or pathway to be discharged.

What are the conditions of such readiness? They seem to be the following: (a) A certain type of stimulus will produce a readiness, amounting to actual discharge, in certain motor pathways. This is the case of the inherited reflex or tropism. (b) A certain type of movement is regularly in a state of heightened readiness; for example, the movements of withdrawal from injury, as is shown by the very rapid learning that punishment produces. (c) Frequency of previous discharge leaves a motor pathway in a condition of heightened readiness; this is shown by the favorable effect of repetition on learning. (d) Immediately after a motor pathway has discharged, there is a short refractory period during which its activity is inhibited, but following this there is for some sec-

onds a fairly high degree of readiness; this is shown by the fact of forgetting with lapse of time. (e) By the law of the conditioned reflex, two stimuli occurring together (and "together" here means not merely at the same mathematical instant, but within a period of some seconds' length) acquire the power each to set in readiness the movement which originally resulted from the other stimulus. If the two movements in such a case are incompatible, like coming forward and running away, that one will survive *which already possessed the greater degree of readiness*. This is shown by many cases of learning. (f) By a special case of conditioning, the performance of one movement may set in readiness another one which has occurred together or nearly together with it. Here the kinæsthetic excitations resulting from the performance of each movement condition the performance of the other. This is shown by learning of the movement system type. (g) The presence of certain internal physiological states sets in readiness motor pathways leading to movements that put an end to these states. Such states constitute the "drives," whose importance we have seen.

The degree of readiness may be so great that it passes over at once into actual discharge and the full performance of the movement. Or it may be so slight that it merely facilitates discharge when the proper additional stimulus comes along. Or it may be of an intermediate degree such that it produces slight, incipient, tentative performance of the movement.¹ We have been assuming that the anticipatory or incipient performance of movements is what underlies the memory idea.

The most puzzling problem connected with learning is this: How can the results of an action increase or diminish the tendency to perform whole series of movements that preceded the action in time? How, for example, can food at the centre

¹ The physiologist will have no difficulty in reconciling these facts with the "all-or-none" principle, according to which nervous elements discharge either completely or not at all: incipient and full movements may differ in the number of nervous elements involved or the duration of their action, or both.

of a maze operate to eliminate wrong turnings at the entrance? This is a case where the end "suggests" the means, which seems as though an effect were to produce a cause.

Now it appears from our experimental evidence that this process occurs only when the readinesses involved result from a drive. Szymanski's observation that a rat will not learn a maze with food in the centre if he is not hungry, and that after he has learned it he will not run it correctly unless he is hungry will be recalled (see p. 325); also the writer's experiments showing that while speed of movement of white mice in a maze may result from either hunger or from general activity, only the speed resulting from hunger is correlated with the elimination of errors. Further, a rat will run a given maze only under the influence of the drive that made him learn it (959).

The peculiar nature of a drive, then, must have in it something that will explain the process which Thorndike called the "stamping in" and "stamping out" of movements by their pleasant or unpleasant consequences, their success or failure in satisfying the drive; and the hardest thing to explain about this process is its backward direction. So difficult is it to make the processes of association, as far as we can conjecture their physiological character, explain this backward direction, that vitalists such as McDougall (625) derive from the difficulty a strong argument for regarding the peculiar "something" in a drive as a unique and mysterious principle inherent in living matter as such, and never to be explained by the ordinary laws of physics and chemistry.

We shall try in this section, not, indeed, to arrive at a complete physiological theory of learning, which must be constructed by a physiologist when physiology has discovered the nature of the nervous process and the manner of its transfer from one neurone to another, but to see whether the central difficulty, the nature of a drive, can be expressed in physiological terms, or is really of such a character that physiology can never hope to solve it.

The hardest thing to explain about a drive, we have just said,

is its backward direction, the fact that food at the end of a maze makes an animal readier to perform a turning at the beginning of a maze. Now we have seen that backward association over very short intervals seems to occur almost as readily as association in the forward direction. Besides the evidence obtained by Mueller and Schumann that nonsense syllables can be learned more quickly in one sequence if they have been previously learned in the reverse sequence, we have more recent proof from the experiments of Yarbrough. It will be recalled (pp. 268f.) that he trained rats to turn around in a pathway when given an electric shock. When they had acquired this habit, an electric buzzer was sounded before the shock was given, or, in other series, an electric light was shown as the warning stimulus, and the rats finally learned to turn around at the buzzer or the light without waiting for the shock. The point which concerns us is that they learned about as easily to turn at noise or light when in the training experiments these had *followed* the shock as when they had preceded it, provided that the interval did not exceed one second. With longer intervals the association was much harder to form in the reverse than in the forward direction. A reverse association with so short an interval can be explained as easily as a forward association: we have only to suppose that the effect of the first stimulus persists while the second one acts, so that the two are virtually simultaneous.

When, then, the rat as a result of finding food at the centre of a maze learns to take the right instead of the wrong turn at the entrance, although even with his fastest running the initial turn precedes arrival at the food by fifteen seconds, we might conceive that the readiness of the last movement in the series is transferred back to the movement just preceding it, the readiness of this movement back to its immediate predecessor, and so forth. The thing is not impossible, but why should not the last movement suggest rather what happens next after the food; being taken out of the maze, for example?

We must look more closely at the nature of a drive. It

will be agreed, I think, that a drive is a state of physiological unrest, due either to a lack or a superfluity of certain physiological substances: such, at least, is the mechanistic view, while the vitalist considers it a manifestation of a mysterious life force. The first effect of such a situation seems to follow the law of forward association, and to set in readiness the movements that have oftenest followed it, namely, the movements that have put an end to it. For example, when we have been without food for a certain time we feel sensations of hunger. These sensations, it has been shown, are produced by contractions of the stomach similar to those involved in the process of digestion which occurs in the actual presence of food. Thus the physiological condition due to lack of food sets in readiness, amounting to actual performance, those movements which have regularly followed it, and which if food is present have put an end to it. But what happens if food is not present? The physiological state continues. What more natural than that it should set in readiness any and all movements that have within a fairly recent period accompanied it? This would mean, that if an animal while in a state of hunger has recently performed the movements of running the maze, the next time he is in a state of hunger the maze running movements will naturally be suggested, and if the maze is there he will run it, until the state of hunger ceases, that is, until he reaches the food. On this principle an animal that is hungry will tend to do anything that he has recently done when hungry. The beginning as well as the end of the maze running process is associated with the drive because a drive is not a momentary stimulus like a sound or an electric shock, but a persistent physiological state that is present through the whole running. Much of the mystery of the backward direction disappears when we remember this fact.

But if this were the whole story, then the maze would indeed be run every time the rat was hungry, even though there were no food in it, on the same principle that a man who is in a state of nervous irritation forms the habit of twisting a

coat button. But *it would not be learned*; that is, there would be no dropping off of wrong turnings or blind alleys. It is the putting of an end to the drive when the centre of the maze is reached that produces the elimination of errors.

In what order are the parts of the maze learned? The evidence is not wholly clear, because the maze situation is complex, but as the reader will recall, on the whole it indicates that the part nearest the food is acquired first. Tolman has shown further that of two blind passages in a maze, the longer one is eliminated sooner than the shorter one; and he has also demonstrated that if, in two passages of equal length, the rat can be detained in mid-course for different lengths of time, he will quickly come to choose that passage in which the delay period is shortest (see p. 279). It seems, then, that we can describe the phenomena of learning through the influence of a drive somewhat as follows. The drive itself is a condition of unrest produced by too little or too much of some substance of physiological importance. This sets in readiness first those movements which have habitually followed it and put an end to it; as for example the stomach movements and the flow of saliva, or chewing movements, in the case of hunger. If these do not put an end to it, because some further stimulus such as food is lacking, the physiological state extends its influence further and sets in readiness those movements which have on former occasions occurred just before it came to an end. The process goes thus backward rather than forward, setting in readiness the last movements of the maze rather than the movements made by the rat just after it had finished eating, because the drive, which is persisting as a stimulus, is of course much more strongly associated with the movements made in the maze while it was operating on the previous occasion, than with anything done after it had come to an end. If the last movements before getting food can be actually made, the food is reached and the drive ceases; if they cannot, because the rat is not at the proper place to make them, the drive con-

tinues and extends its influence still further backward to the movements which just preceded the last ones, and so on back.

Three statements appear to be true of a drive. (1) Its effective duration seems to be longer than the effective duration of an external stimulus. If an external stimulus lasts a long time its effectiveness is diminished by processes of sensory adaptation and fatigue of muscular adjustment; a drive, as an inner physiological state, may also lapse or be interfered with by some other incompatible state, but not so readily. The organism is built to ignore unchanging external conditions, but to experience persistent inner states until the physiological balance that is interfered with is restored. (2) By the ordinary principle of association, on a later occurrence, a drive may set in readiness any movements which occurred while it lasted on a previous occasion. (3) The facts show that it will set most strongly in readiness those movements which most immediately preceded its resolution on a previous occasion. This "gradient" of excitation from movements just before the final "success," step by step to those at the beginning of the series, may also be explained by the ordinary associative laws. The movements nearest the end of the series have a greater readiness due to recency of performance. Further, the drive itself may be supposed to be strongest just before it is put an end to by the redressing of the physiological balance.

When, it thus appears, the physiologist is ready, through having worked out the problem of the physico-chemical nature of the nervous process and the process by which it is transferred from one nervous pathway to another, he need fear no especial difficulty arising from the nature of a drive, which will compel him to forsake the mechanistic creed.

The sequence of events as we have conceived them in the case of an animal learning a maze may be similarly conceived in that of a man working out a problem in his mind. In both cases there is a persistent and uneasy drive; in both cases this suggests movements that have previously accom-

panied it, and introspection tells us that we first think of immediate means of solving the problem, and only later pass to more indirect methods.

Finally, substitutive and system-forming learning can be brought under a common head if we take into account the presence of the drive in system-forming learning. In our previous discussion, it seemed as though these two types involved different laws of nervous action. In substitutive learning one movement is dropped out, giving place to another of more vital importance; in system-forming learning no movement is dropped out, but each movement, after the first one, gradually comes to do without the external stimulus that originally produced it, and to be sufficiently stimulated by the sensory excitations resulting from the performance of the preceding movement. Now if the situation is analyzed a little further, it appears that system-forming learning is really a special case of substitutive learning. Before the movements have become organized into a system, before the maze (or the alphabet) has been learned, the sensory excitations resulting from a movement do not bring about any definite motor response. The child says "A," and the contractions of its speech muscles produce kinæsthetic sensory processes, but these have no definite effect in determining another movement. As a result of the learning process, to these kinæsthetic excitations, in place of no definite response, there is attached the response of pronouncing B. Thus the process is analogous to the typical case of substitutive learning, where the sound of the trainer's voice loses its original effect of producing fright reactions and substitutes the effect of making the animal come for food.

But in substitutive learning the surviving response survives because it is prepotent, that is, has greater readiness. And this is true also in system-forming learning, but *true by virtue of the drive*. In system-forming learning, the kinæsthetic excitations resulting from the first movement of the series would never lose their original vague and diffused effect

and substitute for it the production of the second movement, if the second movement were not prepotent, that is, already in readiness. And the cause of its readiness is its association with the persistent drive which accompanies the whole series. Thus we may venture to say that system-forming learning never occurs except under the influence of a drive. Substitutive learning may easily do so, especially if the victorious response has what we may call the inherent readiness of the negative reaction to punishment. An animal need not be under the influence of a drive to learn to avoid seizing a second time something that has hurt it the first time. But all cases where successive movements are organized into a system need the influence of a drive to supply the readiness or prepotence required for the survival of the movements. The little ground squirrel which had learned to run to a certain spot and then climb, so that the succession of movements was automatic (see p. 281), had formed this habit under the drive of the bodily uneasiness that sent her to seek her offspring.

CHAPTER XII

SOME ASPECTS OF ATTENTION

THE student absorbed in reading "does not hear" an approaching footstep. That is, a stimulus which would under other circumstances produce an effect loses a great part of its influence because of the fact that another stimulus is already upon the field. This other stimulus need not be more intense, that is, need not involve more physical energy, than the one which is ignored. It does not win the victory by a mere swamping of its rival through its superior quantity. A man may walk along city streets, his eyes and ears bombarded with brilliant lights and loud sounds, and yet the centre of his consciousness may be a train of ideas, representing in their physical accompaniment in his cortex a quantity of energy insignificant compared with that of the external stimuli pouring in upon him. Psychologists commonly express this fact by saying that while the strength of a stimulus conditions the intensity of the mental process accompanying it, the *clearness* of that process depends upon *attention*.

§ 85. *The Interference of Stimuli*¹

Attention, then, is the name given to a device, whatever its nature, whereby one stimulus has its effectiveness increased over that of another whose physical energy may be greater. What happens in the simpler forms of animal life

¹The meaning here ascribed to this expression should be distinguished from the fact, discovered by Heymans, that two stimuli acting on the same organ simultaneously may inhibit each other to some extent. Spencer (939) has shown that a rat's sensitiveness to a spot of faint light was diminished if a bright light were thrown on another part of the visual field, the effect increasing in direct proportion to the intensity of the bright light.

when two stimuli, requiring different reactions, operate simultaneously? We may quote from Jennings the facts about *Paramecium*. "If the animal is at rest against a mass of vegetable matter or a bit of paper, . . . and it is then struck with the tip of a glass rod, we find that at first it may not react to the latter stimulus at all." "A strong blow on the anterior end causes the animal to leave the solid and give the typical avoiding reaction." "If specimens showing the contact reaction are heated, it is found that they do not react to the heat until a higher temperature is reached than that necessary to cause a definite reaction in free-swimming specimens." "On the other hand, both heat and cold interfere with the contact reaction. *Paramecia* much above or much below the usual temperature do not settle against solids with which they come in contact, but respond instead by a pronounced avoiding reaction." "Specimens in contact with a solid react less readily to chemicals than do free specimens. . . . On the other hand, immersion in strong chemicals prevents the positive contact reaction." "The contact reaction may completely prevent the reaction to gravity," and to water currents. It also modifies the reaction to the electric current. While a part of the influence exerted by the contact reaction on other responses may be purely physical, due to the fact that an actual secretion of mucus may occur whereby the animal "sticks fast" to the solid, yet this alone does not explain the facts, for the cilia that are not attached do not behave normally. The reaction to gravity regularly yields whenever opposed to the action of any other stimulus (512, pp. 92 ff.).

Sometimes the action of one form of stimulation merely affects the form of the response to another, as in the case where abnormal temperature causes the avoiding instead of the positive reaction to be given to solids. In other cases, reaction to one of the stimuli is suppressed or weakened. The facts suggest that the influential stimulus is either the *one that is on the field first* (the contact reaction may prevent

response to temperature, or abnormal temperature may modify the contact reaction), or the *one that is the more important* (gravity yields always to other stimuli).

In some higher animals the effects of interference of stimuli have been noted. The earthworm will not respond to light if feeding (229) or mating (453). In the turbellarian *Convoluta roscoffensis* light is victorious over heat in determining reaction. The animals in their positively phototropic phase will remain in the heated light end of a vessel until they perish. Light and gravity are more nearly balanced in their effects. *Convoluta* is negatively geotropic, yet if the brightest region is below the surface, the animals will go there. But if this region is only a little brighter than the surface, they will stay at the surface, gravity dominating (342). The sea-urchin shows in its behavior a somewhat similar relation between mechanical and chemical stimulation. If weak acid is dropped into the water containing specimens of *Arbacia*, their spines begin to interlace. A slight shaking will restore them to the normal position, but if more acid be added, no mechanical stimulation will overcome the effect of the chemical (999). Various facts concerning the interrelations of gravity and light as stimuli have been noted in Chapter VIII. A very interesting case of the suppression of one reaction by another is reported by Holmes in his observations on the water insect *Ranatra*. The positive response of this insect to light, very precise and striking, may be wholly suspended when the animal is feeding, when a number of individuals are collected, when the insect stops to clean itself, or even "by the sudden appearance of a large object in the field of vision," behavior which is strongly suggestive of the "distraction of attention" in a human being (461). Holmes (463) also observed that the fiddler crab, although it ordinarily moves towards the light, would run away from a moving light, fear overcoming positive phototropism. Roubaud, in a study of the behavior of some species of flies that live on the seashore, feeding on dead fish and the like, says

that they will abandon the "head on" position which they regularly assume toward the wind, if attracted by the odor of food (878).

Revesz (860) explains the superiority of fowls over monkeys in learning to make certain visual discriminations connected with food, by the fact that the fowl's reactions are under the conditions in question wholly determined by food and by visible objects, while the monkey's are at the mercy of a much wider variety of stimuli.

Wherever we find that one class of stimuli regularly yields to another if the two act together, it is safe to assume that the prepotent stimulus is more important to the organism's welfare than the vanquished one. And while we cannot without more ado call such cases of the interference of stimuli as are found in very simple animals cases of attention, and ascribe to their psychic accompaniment all the characteristics of attention as a feature of our own experience, yet we may assert that they have in common with attention the significance of being *a device to secure reaction to the most vitally important of several stimuli acting at once upon the organism.*

§ 86. *Methods of securing Prepotency of vitally Important Stimuli*

An inanimate object acted upon by several forces at once is determined in its motion by their relative intensity. Conceivably, an extremely simple form of animal life, when subjected to two stimulations acting together, would also respond in a way answering precisely to the relative strength of the two. It is easy to see what would be the disadvantage of such a state of affairs for the animal. The weaker of the two stimuli might be of far greater significance for organic welfare than the stronger. For example, it would often be important that an animal should be able to respond to a very faint food stimulus rather than to any of the stronger

forces acting upon it. Evidently a prime need of animal life is some arrangement whereby weak but important stimuli shall be given the preference in determining reaction over stronger but less vitally necessary ones. *Sense organs* are one such device. The comparatively slight amount of chemical energy coming from a bit of food may have its effectiveness for the nervous system greatly increased through its reception by a structure adapted to use the whole of it to advantage. Light stimulation involves a quantity of energy that is insignificant in comparison with the grosser forces acting on an organism; yet falling on the retina, the energy is economized and magnified through the stored-up chemical forces it sets free. Thus a weak stimulus may by a sense organ be made powerful to determine reaction. Another arrangement to the same effect is the peculiarity of the nervous system whereby, through an arrangement akin to the summation of faint stimuli, *a moving stimulus*, one acting successively upon neighboring points of a sensitive surface, *produces an effect disproportionate to its intensity*. A moving stimulus is a vitally important stimulus; it means life, and hence may mean food or danger. The response to it is in most cases adapted rather to its importance than to its physical strength. A third arrangement for the securing of reaction to vitally important stimulation lies in the existence of *preformed connections* in the nervous system, which bring it about that the *path of the excitation produced by one stimulus is clear to the motor apparatus*, while that of another is closed. Reactions of this sort we call instinctive. The nesting bird responds to the sight of building material rather than to that of objects offering equally strong stimulation to the optic nerve; the cat sits at the mouse hole, the parent animal responds to the faintest cry of the offspring, because these stimuli have the right of way by virtue of inherited nervous connections.

Finally, a weak stimulus may determine reaction and be victorious over a stronger one because of *nervous pathways*

formed through the individual's own experience. The consequences of reaction to it in the individual's past may operate to secure reaction to it in the future. To the cat in a puzzle box, the string that must be pulled to let it out offered originally no stronger stimulus to action than any other object in sight; but after sufficient experience the string comes to dominate the situation and determine the cat's behavior. If the experience of consequences is slowly acquired, by many repetitions, the process of reacting to an object originally indifferent may be unaccompanied by any ideas of the consequences of such reaction. If it is rapidly acquired, we know that we human beings at least accompany our reactions by calling up the results of our past reactions in the form of memory ideas.

§ 87. *The Peculiar Characteristics of Attention as a Device to Secure Prepotency*

We have suggested that attention is a means of securing reaction to the vitally important stimuli acting upon an organism. Does reaction to a stimulus always mean attention to the sensation accompanying that stimulus?

This question may best be answered by examining the characteristics of the attention process as we know it. In attention, the details of the object attended to become clear and distinct. That is, attention is a state where discrimination is improved. Further, attention involves varying degrees of effort, and these are marked by varying intensity of certain bodily processes. Attention under difficulties is accompanied by a rigid position of the body, by holding the breath, and by various muscular effects, aside from the processes which, like frowning, are concerned with the adaptation of the sense organ to receive an impression. These general bodily effects of attention are all such as to suggest that the body is to be kept as quiet as possible during the attentive state. In other words, no reaction is to be made to the object at-

tended to except such as may be necessary to allow its being carefully discriminated from other objects. *Attention, in its intenser degrees, at least, seems to involve a state of suspended reaction.*

Not every case, then, of response adapted to the vital importance of a stimulus is a case that suggests as its psychic aspect attention to the accompanying sensation. When, for example, a reaction of especial speed is made to contact with a moving stimulus, the speed of the reaction would itself indicate that the sensations produced are not attended to. The proper situation for attention would be the situation in which the reaction needs to be suspended until the stimulus is fully discriminated. Now such careful discrimination does not appear to be characteristic of reactions that are largely based on inherited nervous structures. Many facts concerning the instincts of animals, that is, their inherited reactions, indicate that these are extremely rough adjustments of behavior to environment until refined by individual experience. Hudson observed, for example, that newly born lambs on the South American plains had a tendency to run away from any object that approached them, and to follow any object that receded from them. They would follow his horse for miles as he rode along, and would run away from their own mothers when the latter moved toward them. He explained this as adapted to the fact that ordinarily their first duty, on making their appearance in the world, is to keep up with the receding herd, while an approaching object is more likely to be an enemy (476). Later, this rough adjustment is modified; they learn by experience not to run away from their mothers, and not to follow indiscriminately any leader.

If it is true that instinct unmodified by experience is adapted to general rather than to special features of environment,¹ it seems likely that the phenomena of attention as we

¹ In this connection Franz's experimental demonstration that the frontal lobes, long regarded as the seat of the neural processes under-

know them are found chiefly in connection with those responses to vitally important stimulation which are determined, in part, at least, by the individual experience of the reacting animal, for these are the responses requiring most careful discrimination among stimuli, and the delay of reaction until such discrimination has been made.¹ Putting the matter in a slightly different way, we may say that purely inherited responses can be adapted only to certain broad, roughly distinguished classes of stimuli, for these alone are common to the experience of all members of the species. Nothing but individual experience can bring to light the importance for welfare of certain particular stimuli, for the significance of these would vary with the experience of each individual animal. Among the lower animals, attention probably reaches its highest pitch where the response most needs to be suspended in order that the stimulus may be fully discriminated. The rabbit or wild bird crouching motionless close to the ground, watching each movement of a possible enemy, suggests strongly to our minds a condition of breathless attention. Whether such an interpretation is the true one depends very much, I should say, on the extent to which past individual experience has refined the animal's powers of discrimination. Mere "freezing to the spot" may be an inherited reaction, useful in time of danger, but more analogous in its psychic aspect to the blank emptiness of the hypnotic trance than to alert, watchful attention.

Yet although, in so far as attention is a state favoring discrimination of stimuli, it is involved in that part of an animal's behavior which is derived from individual experience, since pure instinct discriminates but roughly; in so

lying attention, are concerned in the functioning of recently learned reactions, is of especial interest. Franz found that cats and monkeys which had been trained to work mechanisms lost the power to do so when the frontal lobes were extirpated, although habits of older date, such as responding to a call, were preserved (463, 464).

¹The tendency of much recent discussion of instinct is to reject the congenital factor altogether and explain everything as the result of experience.

far as it is still one of the devices for securing reaction to stimuli of vital importance, its root must lie in instinct. No object wholly unrelated to some fundamental drive can hope to secure attention, for the great classes of vitally important stimuli have all of them preformed paths in the nervous system by which their reactions are secured. What individual experience does is to refine upon the adaptations which instinct makes possible; to bring about the connection of certain stimuli, originally indifferent, with the performance of an instinctive response, or to produce a checking of the instinctive response when certain individual peculiarities of a stimulus that would otherwise call it forth become evident. For instance, an animal learns by experience to come at the call of a human being who feeds it; the sound, originally without effect on its reactions, has come to be connected with the nervous mechanism of an instinct. The chick pecking at small objects on the ground learns by experience to inhibit this instinctive response with reference to objects having certain peculiarities originally undiscriminated, but now in some way emphasized through painful circumstances accompanying his previous encounter with them.

The most fundamental characteristic of attention, then, is perhaps that aspect of it which has been called *abstraction*, the diminished effectiveness of stimuli not attended to. By virtue of this aspect we recognize that attention belongs with instinct as being concerned in securing the prepotency of vitally important stimulation. On the other hand, the further characteristic of attention; namely, that it is a state of suspended reaction involving careful discrimination of stimuli, suggests that its functioning is connected rather with the refining and modifying influence of individual experience acting on instinct, since here alone do we find delayed reaction and accurate stimulus discrimination.

The highest grade of attention, the final triumph of vital importance over mere intensity of stimulation, is to be found where the focus of attention is occupied by an idea or train

of ideas. When a process purely centrally excited holds the field and makes the individual deaf and blind to powerful external stimuli pouring in upon his sense organs, then he is superior to the immediate environment at least. This form of attention occurs, probably, only when the vital importance of the idea attended to has been learned through that most rapid form of individual acquisition of experience which involves the revival of the past in idea. It has been called derived attention. The ideas attended to are held in the focus of consciousness and analyzed through the power of associated ideas. The inventor holds to his problem, the student to his task, in spite of distractions, because of the consequences which he thinks of as likely to result. It seems unlikely that attention in this final form occurs among the lower animals. While ideas are probably present to some extent in the minds of the higher mammals; they are hardly so far freed from connection with external stimuli that the animal can shut out the world of sense from its consciousness and dwell in a world of ideas.

CHAPTER XIII

THE ANIMAL MIND

How, finally, shall we describe the mind of an animal? What is the inner aspect of its behavior; what, to use the configurationist's metaphor, are the figures and grounds of the patterns of its consciousness; how does the world look to it? This question, of course, must be answered in detail differently for each animal species. But our discussion in the preceding chapters has brought to light certain general factors that will determine the nature of the answer. These we may now summarize, and as we do so, certain typical forms of animal consciousness, or stages in the development of the animal mind, will suggest themselves as the natural result of their operation.

(1) First of all, we must consider the influence of *general physiological condition*, which determines the background of consciousness and also, as we have seen, to a large extent what shall appear against the background.

Rest and activity: such are the most fundamental alternations in the physiological state of an animal that express themselves in its external behavior. The conscious correlate of the beginning state of rest we ourselves experience as pleasurable relaxation. As the state of rest continues, consciousness, whose essential condition is change, lapses. The condition of activity is set up sometimes by internal processes, and evidently the readiness with which it is thus set up depends on "the nature of the beast." In creatures like lions and tigers, which need to use great physical force, rest seems to accumulate energy which, if it cannot be worked off, must produce a highly unpleasant background. In animals built

for long periods of activity, like *Paramecium* or fish, the activity would become purely automatic and cease to be conscious. Often activity is the result of a specific drive like hunger or sex; its conscious coloring would then be unpleasant, and would carry with it sensations obscurely felt from some bodily region. On the other hand, activity may be caused by the action of an external stimulus; an unfavorable condition being set up by temperatures or light intensities above or below the optimum; a background of general unpleasantness would accompany such restlessness. Sometimes it is the kinetic effect of light that keeps animals whose normal state is one of activity, like small flies and midges, at their whirling dances, which we naturally think of as not unpleasant in their conscious accompaniment, if indeed their steady continuance does not make consciousness lapse. Long continued activity would bring into the background the unpleasantness of fatigue.

(2) Secondly, the *nature of the receptive surface* of an animal's sense-organs will determine what sensation qualities emerge from time to time on the background provided by the general physiological state.

The transparent bodies of the lowest animals allow the light-waves to pass through them, and we have seen that an early theory of the tropism holds that the animal's body is affected by the direction in which the light traverses it. Other forces, such as heat, mechanical vibrations, electrical waves, may pass through the body. But certainly very early in the development of life it became a function of the body surface to prevent external forces from getting inside; to secure reaction to them before they have a chance to enter. We need only remind ourselves of the wonderful mechanism through which the internal heat of our own bodies is kept constant while the surface heat varies so greatly. Even the transparent *Amœba* reacts to light as soon as the tip of a pseudopod comes into contact with it.

The earliest discrimination among the stimuli that strike

the surface of the body is that between the harmful and the harmless. Usually the point affected is withdrawn from contact with a harmful stimulus, and makes no reaction at all to a harmless one. The difference between the consciousness accompanying the restlessness of an animal subjected to an unfavorable stimulus all over the body surface, such as heat, or in such physiological conditions as hunger or fatigue, and the consciousness accompanying the negative reaction to local injury, corresponds to the difference in our own experience between general unpleasantness and localized pain. Next in order of development is the discrimination, among harmless stimuli between food and not-food. The receptive surface has been so modified that it is specifically affected by the chemical character of certain organic substances: food is swallowed, not-food is ignored or rejected. Whatever the peculiar substance or structure in the sensory surface that is responsible for this difference in reaction, it will not function unless the proper physiological state is present, for most animals if not hungry will reject food and not-food alike, and many if very hungry will swallow both indiscriminately.

All animals, even the simplest, whose behavior is known to us, seem to have some ability to respond to forces coming from a distance. This really means, of course, merely a high degree of sensitiveness on the part of their receptive surfaces. Chemical particles diffused through water or air from a distant object will be less concentrated than those of an object in contact with the body; a smaller quantity of light rays, other things being equal, reaches the body from a distant than from a near object, and so forth. Even *Amœba*, it will be remembered, senses food and light a few thousandths of a millimeter away. But in the higher animals this sensitiveness is still further refined, and at the same time the sensory substances are more differentiated. Besides the food quality of the chemical sense, a sex quality is developed and perhaps, as in ants, an enemy or foreigner quality; the food quality itself differentiates itself into several. The original light sen-

sation of brightening or darkening has added to it sensations of qualitative change, as the altered wave-length of the light affects the photoreceptive substances differently. The sensations of jarring, set up through the motion of statoliths, are further refined by an apparatus that responds to finer air vibrations: first, probably, only to those produced by animals of the same kind but opposite sex; first, as undifferentiated noises and only much later as tones.

On the background, then, of dim awareness of general bodily condition, there emerge from time to time in the animal's consciousness flashes of different quality, food, pain, mate smell, brightening, darkening, jarring or tipping; in more highly developed animals something corresponding to color differences and sounds, mostly mate sounds. It has often been said that a pure or isolated sensation quality is an abstraction, but in the mind of an animal too lowly organized to be capable of space perception, we can imagine flashes of pure quality, modified only by the background of organic sensation. Always the background of physiological state must be reckoned with; it helps to determine which stimulus shall be prepotent. Food sensations will be faint or lacking if the animal is not hungry; mate sensations if it is not at the right period of its reproductive cycle. Sensations of injury would be least subject to fluctuations in the physiological background, yet even they may vanish from the field when the drives of fighting or mating are dominant.

The response of the sensory surface to stimulation weakens, and the sensations disappear, if the stimulus is long continued or often repeated; the receptive substances become exhausted. Here again injury is probably able to maintain its effectiveness as a stimulus longest.

(3) Along with inner physiological state and development of surfaces receptive to external stimuli, the third great factor in the animal mind is the animal's *capacity to move*. This may be considered under six headings: (a) movement of

the whole body, (b) movement of a sense-organ, (c) movement of a grasping organ, (d) the modification of one movement by another, (e) suspension of movement, (f) language.

(a) An important influence on the mind of an animal is exerted by the speed with which the animal can get from one place to another. We have just noted the effect of activity on the background of consciousness, and we may now note that the flashes of sensations against this background will come in quicker succession if the animal is in rapid motion. On the other hand, it will run easily into danger, and will need a negative response so quick that the ability to delay reaction must be sacrificed, and along with it fine discrimination of sensation qualities and recall of memory ideas. The ideal condition for intellectual development will require that an animal shall habitually move neither too slowly to get variety of stimulation nor too fast to pause from time to time for discrimination and recall. Swift movement should be, as in birds and bees, punctuated by pauses.

(b) The value of the pause is partly that it allows time for movement of the sense-organ. As we have seen, a movable sense-organ seems to be the main requisite to enable an animal's conscious experience to take on spatial structure. A moving stimulus, it is true, can probably produce a sensation of unique quality by virtue of the fact that it moves, if the sense-organ has an extended surface whose points can be successively affected, even though the organ is immovable. There is evidence from human psychology that the sensation from a moving stimulus is unique; for example, if a person is touched by a point which moves just a little, the fact that it moves will be recognized even though he cannot tell in what direction it moves. The quality of movement should be added to the list of "flashes" mentioned under (2), page 351. But a moving sense-organ, as we saw in Chapter IX, can give a reversible series of sensations, such as is indispensable to the existence of a true space perception. If your

organs of smell are movable and can explore a surface, you can perceive smell patterns; if your eyes are movable, you can perceive visual patterns. Thus in place of flashes of sensation there will be orderly arrangements of sensations simultaneously perceived. It is possible that the existence of a fovea in certain vertebrate eyes, that is, a region where vision, defective elsewhere, is clearest, may bring about a better analysis of the visual field than would occur if vision all over the retina were as good as foveal vision; since the fovea forms a central point of reference, a terminal point, for all eye movements. The only substitute for moving the sense-organ that suggests itself would be moving the whole body if the sense-organ were large and the body small: in this way wasps and bees, though their eyes are fixed, may get their undoubted capacity for visual space-perception.

(c) After patterns, objects or things. These are patterns which change their position independently of other patterns. When the animal itself moves, the whole visual field (or smell field) moves in the opposite direction, and in this case is likely to remain in the status of unanalyzed background. Sometimes when the animal is at rest, a pattern will detach itself from the background and change its position; it thereby acquires the status of a thing. But as we have seen, a pattern becomes a thing most permanently and completely when the animal can move it; when the animal has a grasping organ by which it can alter in many ways the arrangement of its background patterns.

(d) The formation of patterns and of things is of course profoundly modified through the influence exerted by one movement on another. By the mutual influence of movements in substitutive learning, certain features vanish and are replaced by others; through system-forming learning new and more complicated mental structures are formed and held together. *Analysis* of the environment into sensory qualities depends on the nature of the sense-organ surface; into patterns,

on the capacity of the sense-organ to move; into objects, on the use of a grasping organ. *Synthesis* of the results of analysis into new combinations depends on system-forming learning.

(e) As we have also seen, the condition for the highest stage of mental development, that where memory ideas can be used, is the power of an animal to suspend reaction. Not to *cease* reaction, but to suspend it: mere failure to react to a stimulus situation would mean nothing positive either for behavior or consciousness. The reaction must, through the period of suspense, remain in heightened readiness. If it does so, its rehearsal through the interval can produce similar rehearsals of associated movements, and in consciousness the revival of ideas and the development of a plan.

(f) But ideas will be few and simple, and the reconstruction of the environment will be crude, unless there is language. For developed language, one must have a repertory of diversified movements that can serve as symbols, so that one of them functions in place of a whole group, as the word "vertebrate" functions in place of a long description of anatomical features. And the movements of this repertory must require little physical effort, and must not interfere with locomotion or bodily posture. Small and complex muscular systems are required, such as are found chiefly in the grasping organs and the vocal organs. The hands of man, with their opposable thumbs, are capable of far more complex movements than those of any of man's near relatives; perhaps a comparative study of the vocal muscles of the anthropoid and the human infant will show why man articulates so much better than the ape.

Through every stage of the development of the animal mind, in modifying the nature of the background of consciousness, in determining the appearance and disappearance of such sense-qualities as the sense-organs can furnish, in the formation of complex mental combinations through system-forming learning, and in suspending reaction long enough to allow the

formation of patterns through the use of a movable sense-organ, of objects through the use of a grasping organ, and of ideas through the incipient performance of the response during the delay period, the dominant factor is the drive.

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INDEX OF SUBJECTS

- Abstraction, 346. *See* Analysis of situations.
 Accommodation of lens, 234 f.
 Acephala, 72, 130.
 Actinia, 200, 254, 259.
 Actinobolus, 62.
 Action currents, retinal, 139 f., 143.
 Activity, effect of, 201, 325 f., 348 f.
 Adamsia, 63, 254.
 Adaptation, as evidence of mind, 26; emotional, 255 f.; sensory, 253 ff.; to color, 163; to darkness, 162 f.; to light, 195 f.; to rotation, 285.
 Aeolosoma, 71.
 After-images, negative, 163 f.
 Age, effect on learning, 317.
 Aiptasia, 65, 210, 254.
 Aletrion, 72.
 Allolobophora, 70.
 Alternation problem, 306 f.
 Amblystoma, 100.
 Amoeba, 34 ff., 51, 349; mind of, 40 ff.; reaction to colors, 139; to light, 125 f.; to localized stimuli, 167.
 Amphibia, chemical sense, 100 f.; hearing, 118 f. *See* Frog, Salamander, Toad.
 Amphioxus, chemical sense, 97 f.; light reactions, 132 f., 182 f.
 Amphipods, 186, 201, 203.
 Analysis of situations, 240 ff.
 Anecdote, Method of, 4 ff.
 Annelids, 252, 286; chemical sense, 69 f.; color vision, 157; hearing, 106; reaction to shadows, 129 f.
 Ant, 8, 79, 252; adaptation in, 255; and ultra-violet rays, 141 f.; food-finding, 83 ff.; hearing, 112 f.; homing, 85 ff., 215, 225, 289; kinæsthetic memory in, 281; learning, 261 f., 275, 286; recognition of nestmates, 89 ff.
 Antennæ, as smell organs, 79 ff.
 Anticipation of movements, 305 f., 310.
 Apes, delayed reactions, 300 f.; insight in, 309 f.
 Arachnids, chemical sense, 77 f. *See* Spiders.
 Arbacia, 340.
 Arenicola, 187.
 Arthropods, chemical sense, 74 ff.; color vision, 157 ff.; rheotropism, 209. *See* Crustacea, Spiders, Insects.
 Associative memory, 28, 246.
 Asterias, 131.
 Attention, 47, 338 ff.; lapse of, 256; to movements, 312 ff.
 Auditory cues in maze, 282.
 Auditory sensation, *see* Hearing.
 Axolotl, 259.
 Background, effect of on phototropism, 202; of consciousness, 348 f.
 Backward association, 268, 332.
 Balanoglossus, 134.
 Balanus, 196 f.
 Barnacle, 196 f.
 Bat, hearing, 124.
 Bee, 239; color vision, 138, 152, 154 f.; form vision, 220; hearing, 113 f.; homing, 94 f., 225, 226 f.; reaction to flowers, 92 ff.; recognition of nestmates, 95 ff.; smell, 80 f.
 Behaviorists, 20 f.
 Bembex, 228 f.
 Binocular vision, 233 f.
 Birds; 322; chemical sense, 101 f.; color vision, 139, 143 f., 160 f.; form vision, 221; hearing, 121; kinæsthetic memory, 281; learning, 269 f., 275, 282; migration, 230 f.

- Bispira, 252.
 Blowfly, 137, 187.
 Branchipus, 132, 205.
 Breathing rate, as evidence of color vision, 140, 144.
 Brightness discrimination, 152, 165.
 Brightness equivalent of color, 149 ff.
 Bunsen-Roscoe Law, 186.
 Bursaria, 61.
 Buscyon, 72.
 Butterfly, 80, 201, vision, 217, 220.

 Calf, color vision, 156.
 Carmarina, 65.
 Carp, 267.
 Cat, 10 f., 319, 345; color vision, 156; delayed reaction, 294, 300; hearing, 124; homing, 289; imitation, 292; learning, 271 ff., 295, 325; visual type, 222.
 Caterpillar, 191, 198; hearing, 112; vision, 219.
 Catfish, 259.
 Centrostephanus, 130 f., 252.
 Cirrepedia, 132. *See* Barnacle.
 Cephalopods, color vision, 139, 140; accommodation, 234.
 Cereactis, 139.
 Cerianthus, 63, 187; geotropism, 174 f.
 Cessation of reaction to repeated stimuli, 251 ff.
 Chemical sense, 57 ff.; in protozoa, 58 ff.; in coelenterates, 62 ff.; in flatworms, 67 ff.; in annelids, 69 ff.; in mollusks, 72 f.; in echinoderms, 73 f.; in crustacea, 74 ff.; in arachnids, 77 f.; in insects, 78 ff.; in Amphioxus, 97 f.; in fish, 98 ff.; in amphibians, 101; in birds, 101 f.; in mammals, 102 ff.
 Chemicals, effect on phototropism, 197 f.
 Chicks, color vision, 153; form vision, 221, 224; imitation, 291; learning, 269, 275, 325; size vision 218; visual reaction to movement, 212.
 Chimpanzee, 300 f., 328; color vision, 153; form vision, 223; insight, 309; perception, 244 f.
 Chlamydomonas, 171.
 Choice, as evidence of mind, 26.
 Chordotonal organs, 109 ff.
 Chub, 150, 151, 322.
 Ciliata, feeding reactions, 58 ff.
 Circus movements, 191 f.
 Clepsine, 129.
 Cockroach, hearing, 109; individual differences, 318; learning, 263 f., 266, 275; vision, 218.
 Coelenterates, chemical sense, 62 ff.; geotropism, 174 f.; hearing, 105 f.; light reactions, 127 ff.; reaction to motion, 210. *See* Jelly-fish, sea-anemones.
 Color-blindness. *See* Color vision.
 Color-perception in monkeys, 244 f.
 Color vision, 135 ff.; in different animal forms, 157 ff.; methods of investigating, 136 ff.
 Conditioned reflex, 266. *See* Substitutive learning.
 Configurationists, 239 ff.
 Consciousness, 20 ff.
 Continuous action theory of tropism, 186 ff., 194.
 Contrast, brightness, 164; color, 164.
 Convoluta, 195, 204, 340.
 Copepods, 76, 197, 204.
 Corixa, 110.
 Cow, 294.
 Cowbird, 269, 275.
 Crab, color vision, 148; decorating instinct, 157; fiddler, 203, 340; green, 75, 274; hermit, 200, 235, 259, 286; homing, 225; horse-shoe, 78, 198; learning, 263.
 Crayfish, chemical sense, 75 f.; light reaction, 212; learning, 274.
 Crocodile, 121.
 Crow, 101, 181, 302.
 Crustacea, chemical sense, 74 ff.; color vision, 146 f., 148, 157 f.; hearing, 106 f.; light reactions, 131 f., 134, 195; Weber's Law, 165. *See* Amphipods, Barnacle, Branchipus, Copepods, Crab, Crayfish, Daphnia, Isopods.
 Cues in maze running, 282 ff.
 Curiosity, effect in maze running, 283.
 Cypridopsis, 198.
 Cypris, 199.

- Daphnia*, chemical sense, 75 f.; color vision, 138, 146 f., 148, 163 f.; learning, 264; light reactions, 132, 141, 162, 186, 196 f., 199.
- Deilephila*, 155.
- Delayed Reaction Method, 293, 299 f.
- Delayed reaction in monkey, 301; in chimpanzee, 301.
- Density of water, effect on light reactions, 197.
- Didinium, 62.
- Difficulties of comparative psychology, 1 ff.
- Difficulty of problem, relation to punishment, 324 f.
- Dina, 129.
- Direction sense, 88, 94, 95, 289.
- Direction theory of tropism, 187 f., 190.
- Discrimination, methods of investigating, 48 ff.
- Discrimination experiments, 264 ff.; interference in, 322 f.
- Distance, perception of, 232 f.; reactions to, 232 ff.
- Distance receptors and ideas, 310 ff.
- Distribution of practice, 319 f.
- Dog, 6 f., 10 f., 240, 290, 315, 319; color vision, 156, delayed reaction, 294, 300; form vision, 222 f.; hearing, 123 f.; insight, 309; learning, 271 ff., 295; perception of things, 239; scratch reflex, 210; movement vision, 212; smell, 102 f.
- Doubleness, perception of, 242 f.
- Dragon-fly, 231, 253.
- Drive, influence of, 323 ff., 354 f.; nature of, 331 ff., 334 ff.; spontaneous, 328.
- Dreams, animal, 14, 270.
- Dropping out of movements, learning by, 257 ff.
- Dryness, effect on light reactions, 217.
- Dysdera, 216.
- Dytiscus, 79.
- Earthworm, 187, 340; chemical sense, 69 f.; hearing, 106; learning, 247, 263, 274; light reactions, 129 f., 140 f., 191 f., 218; reaction to localized stimuli, 168; touch perception, 235 f.
- Ebbinghaus's Law, 308.
- Echinaster, 131.
- Echinoderms, chemical sense, 73 f.; hearing, 106; light reactions, 130 f. *See* Starfish, Sea-urchins.
- Elberfeld horses, 315 ff.
- Electric current, orientation to, 206.
- Electric shock as punishment, 324.
- Elephants, 241.
- Elimination of errors, order of, 277 f.; factors influencing, 278 f.
- Eloactis, 127.
- Emotional adaptation, 255.
- Entelechies, 18.
- Environment, influence in maze running, 283 f.
- Epeira, 235.
- Errors, nature, as evidence against ideas, 294.
- Euglena, 126, 171, 191.
- Evidence of mind, 25 ff.
- Evolutionary writers, attitude toward animal mind, 14.
- Experiment, Method of, 8 ff.
- Extirpating sense-organ, 53.
- Eye, compound, 211 f., 214, 235; simple invertebrate, 211, 213, 235; superposition, 213 f.
- Eye structure as evidence of image vision, 216.
- Fatigue, 253; for colors as evidence of color vision, 148 f.; independent, of sense organs, 54.
- Feeding reactions. *See* Chemical sense.
- Firefly, 193, 301.
- Fish, 233; chemical sense, 98 ff.; color vision, 138 f., 140, 144 f., 145 f., 150 ff., 159 f., 163; distance perception, 232; hearing, 114 ff.; learning, 259 f., 263, 267, 275, 322; rheotropism, 207 ff.; skin sensitiveness to light, 133.
- Flatfish, 144, 145.
- Flatworms. *See* Planarians.
- Flies, 155, 187, 191 ff., 217, 340 f.
- Flowers, attraction of insects to, 92 ff., 158 f.

- Form, tactual perception of, 235 f.; visual perception of, 220 ff., 243 f.
- Fowls, 242, 341; color vision, 151 f., 155 f., 162 ff.; image vision, 219; individual differences, 318.
- Frequency as factor in eliminating errors, 276 f.
- Fright, in maze running, 283.
- Frog, adaptation, 162; color vision, 140, 144; chemical sense, 100; hearing, 119; learning, 263, 275, 277, 282, 324.
- Fruit-fly, 149, 201 f., 209.
- Fundulus, 208.
- Geotropism, 171 ff., 204 ff.
- Gonionemus, 64 f., 128, 134, 195, 210.
- Grasping organ, 241, 353.
- Gravity, orientation to. *See* Geotropism.
- Guinea-pig, 242, 282 f., 317.
- Gull, 101.
- Hans, the clever horse, 315.
- Harmful movements, dropping off, 261 ff.
- Hearing, in amphibia, 118 ff.; in annelids, 106; in ants, 112 f.; in bats, 124; in bees, 113 f.; in birds, 121; in cats, 124; in coelenterates, 105 f.; in crustacea, 106 f.; in dogs, 123 f.; in fish, 114 ff.; in flatworms, 106; in frogs, 119 f.; in insects, 109 ff.; in rats, 121 ff.; in reptiles, 120 f.; in spiders, 108 f.
- Hedista, 200.
- Heightened reaction by repetition of stimulus, 247 ff.
- Helix, 72.
- Heredity of phototropism, 202.
- Hippolyte, 202.
- Holothurians, 74, 191.
- Homing, as evidence of image vision, 225 ff.; in ants, 85 ff., 289; in bees, 94 f., 226 f.; in cat, 289; in limpet, 289; in wasps, 227 ff., 230. *See* Migration.
- Horse, 301 f., 314 ff.
- Hunger, as drive, 325 ff.; effect of, 73, 198, 272; in coelenterates, 66 f., 254 ff.; measurement, 325 ff.
- Hydra, 62, 127, 134, 248 f., 252, 256.
- Hymenoptera. *See* Ants, Bees, Wasps.
- Ideas, 31 f., 41 f., 290 ff., 343, 354; and attention, 346 f.; and insight, 309 f.; anticipatory, 298; evidence against in animals, 251, 290 ff.; evidence for in animals, 296 ff.
- Image, memory. *See* Idea.
- Image vision, 213 ff.
- Imitation, inferential, 292, 298 f.; instinctive, 291.
- Inclined plane maze, 283.
- Incompatible reactions, 321, 323.
- Individual differences, 318; in hunger, 327 f.
- Infancy, and ideas, 313 f.
- Innate connections, 342.
- Insects, 196; chemical sense, 78 ff.; color vision, 158 f.; hearing, 109 ff.; hovering, 209; light reactions, 132, 134, 141 f., 193, 203, 205; visual space perception, 212, 235.
- Insight, 308 ff.
- Instinct, and attention, 346; as rough adjustment, 344.
- Intensity, of drive, effect of, 325 ff.; of light, effect on phototropism, 195.
- Intensity theory of tropism, 188 ff.
- Interactionism, 17.
- Interference of habits, 322 f.
- Interference of stimuli, 338 ff.
- Interpretation of behavior, methods of, 12 ff.
- Isopods, 193.
- Jassa, 197.
- Jellyfish, 64 ff., 127 f., 167, 168.
- Kinæsthetic memory, 281.
- Kinæsthetic sensations, 56.
- Labidocera, 195, 199.
- Lacrymaria, 62.
- Lambs, 326, 344.
- Lamellibranchs, 72.
- Landmarks, 85 f., 95, 225 ff., 288.

- Language, 2 f., 312, 354.
 Lateral line organs, 117 f.
 Learning, 246 ff., 353 f.; as evidence of mind, 28 ff.; effect on attention, 342 f.; general theory of, 239 ff.; in *Amœba*, 43 f.
 Leech, 71, 129, 186.
 Leg posture in phototropism, 193 f.
 Length of pathway and elimination of errors, 278.
 Light, reactions to, 37, 125 ff., 185 ff.
 Light intensity, change of, reactions to, 125 ff., 211 f.; theory of phototropism, 189 ff.
Limax, 198, 248.
 Limpet, homing in, 289.
Limulus, 78, 198.
 Lines, perception of, 221 f., 244.
Lineus, 148.
Littorina, 199, 203, 217.
 Lizard, 121.
 Lloyd Morgan's Canon, 22 f., 242, 264, 290.
 Lobster, 192.
 Localized sensibility, as evidence of discrimination, 53, 66, 71, 72, 97, 129.
 Localized stimuli, 53, 167 ff.
 Local sign, 169.
 Locomotion, effect of, 352.
Lycosa, 216.

Macacus, 156.
 Macromysis, 202.
Maia, 157.
 Mammals, chemical sense, 102 ff.; color vision, 161.
 Maternal drive, 328.
 Mating reactions, 76 f., 81 ff., 111.
 Mayfly, 193, 197 f., 266 f., 318.
 Maze experiments, 273 ff.; stimuli influencing, 282 ff.; transfer of training in, 321.
 Mechanical stimulation, effect on phototropism, 198 f.
 Mechanism, 20, 204, 335.
 Menotaxis, 203.
 Metabolic rate, effect on phototropism, 198.
 Methods of comparative psychology, 4 ff.; of investigating discrimination, 48 ff.; of studying color vision, 136 ff. *See* Learning.
 Metridium, 64, 67, 127, 254.
 Microstoma, 69.
 Migration, fish, 99 f.; bird, 101 f., 230 f.
 Mimicry in ants, 224.
 Mnemotaxis, 204.
 Mollusk, 204 f., 216, 256; adaptation, 252; chemical sense, 72 f.; hearing, 106; light reactions, 130 f., 199, 211. *See* Cephalopod, Slug, Snail, Squid.
 Monism, 17 f.
 Monkey, 241, 242, 243, 312, 341, 345; color vision, 150, 152 f., 156; form vision, 221 ff.; ideas, 307; imitation, 292, 298 f.; learning, 260, 272, 276, 301, 304; perception of things, 244; size vision, 219; smell, 104.
 Mosquito, 186, 253.
 Moth, 82, 111, 155, 164.
 Motive, 49. *See* Drive.
 Motor types, 319.
 Mouse, 152, 164, 232, 326, 328 f.
 Mouse, dancing, 151, 223, 276, 292, 317 f., 319, 321, 325.
 Movable sense-organ and space perception, 237 f., 352.
 Movement, and discrimination, 48 f.; effect on consciousness, 351 ff.; effect on perception, 241.
 Movement systems, 273, 279 ff.
 Moving stimulus, reaction to, 210 ff., 342.
 Multiple Choice Method, 239, 243, 301 ff.
 Muscular memory in homing of ants, 88. *See* Kinæsthetic Memory.
 Myriapods, 219.
 Mysis, 107.

 Nautilus, 213.
 Necturus, 232.
 Negative reaction, 36, 58 f., 69 ff., 248 f., 255 f., 261 ff.
 Nereis, 71.

 Objective terms, 19.
 Oil globules, retinal, 160 f., 163.
 Orang, 304.

- Orchestia, 195 f., 199.
 Organic sensations, 55 f., 110.
 Orientation, bodily, 293 f.; in maze, 279.
 Orienting reactions, 170 ff.
 Otocysts, 105.
 Owl, 160.
- Palaemon, 76, 107.
 Palæmonetes, 107, 197.
 Parallelism, 16 f.
 Paramecium, 58 ff., 168, 173 f., 207, 262, 339.
 Parrot, 121.
 Patterns, 353.
 Pattern vision, 224.
 Pawlow's Method, 52, 123 f., 223.
 Pecten, 211, 216 f., 252.
 Perception of space, 213 ff.; of things, 238 ff.
 Perch, 263.
 Periodicity in phototropism, 149 ff.
 Phidippus, 216.
 Pholas, 131.
 Photinus, 301.
 Photokinesis, 133 ff., 201.
 Phototropism, 185 ff.; influences affecting, 195 ff.; inhibition of, 340; psychic aspect, 202 f.; relation to geotropism, 204 ff.; reversal by experience, 263 f., 266.
 Phoxinus, 99, 152.
 Physa, 72.
 Physiological state, effect of, 73, 247 ff., 324, 328, 348 f.
 Pig, 304.
 Pigeon, 121, 161, 230, 269, 270, 275, 282.
 Pike, 263.
 Planarian, feeding, 68 f.; geotropism, 205; light reactions, 134, 193; reaction to localized stimulus, 168; rheotropism, 207; temperature reaction, 250; vision, 218. *See* Flatworm.
 Plants, phototropism, 190; reaction to color, 187.
 Play, animal, 313, 328.
 Porcupine, 273.
 Porthesia, 198.
 Positive reaction, 36 f., 59 f.
 Practice, distribution of, 319 f.
 Preference Method, 49, 79.
- Prepotency, effect of, 259 ff.
 Prepotent reactions, 258, 336 f.
 Prepotent stimuli, 340 ff.
 Protozoa, chemical sense, 58 ff.; geotropism, 171 f.; light reactions, 125 ff., 189, 197. *See* Amœba, Paramecium, Stentor, Volvox.
 Punishment, effect of, 323 ff., learning by, 262 ff.; strength of, 324 f.
 Pupillar reflex, 139.
 Purity of water, effect on phototropism, 197.
 Putting through action, learning by, 295.
 Puzzle-box Method, 269 ff.
- Qualities, sensation, 22, 351.
- Rabbit, binocular vision, 234; color vision, 156; learning, 267 f., 295, 323; perception of relation, 241.
 Raccoon, 241, 312; color vision, 150; form vision, 223; learning, 260, 267, 272 f., 295 ff., 299 f.; size discrimination, 219.
 Ranatra, 194, 196, 199, 340.
 Random movements in phototropism, 191 f.
 Rat, distance perception, 232; hearing, 121 ff.; learning, 268, and *passim* thereafter; movement vision, 212.
 Reaction time, as evidence of discrimination, 71 f.; differences in, 54.
 Readiness of motor discharge, 329 f.
 Recognition of nestmates in ants and bees, 89 ff., 95 ff.
 Relations, perception of, 241 ff., 323.
 Repetition, Law of, 247. *See* Frequency.
 Reptiles. *See* Snakes, Turtles.
 Response to stimulation as evidence of mind, 25 f.
 Rest, 348.
 Reward, effect of, 266 ff., 323, 325.
 Rheotropism, 206 ff.
 Rhythms, acquired, 286.
 Righting reaction, 171, 175, 176, 179, 181.
 Rotation of maze, effect of, 285.

- Sagartia, 127.
 Salamander, 100 f., 232.
 Salivary reflex, 52, 156.
 Sample, method of choice by, 244 f.
 Sarsia, 127 f.
 Sea-anemone, feeding, 63 f.; learning, 253 ff., 258 f., 286; light reactions, 127, 139, 185, 200; touch, 67.
 Sea-urchin, 138, 169, 340.
 Secondary cues in experiments, 51 f.
 Sense-organs, as evidence of discrimination, 48 f.; and prepotency, 342; influence of, 349 ff.; movement of, 352.
 Sensibility to difference, 133, 186.
 Sensory types, 318 f.
 Serpula, 138.
 Sex differences in learning, 318.
 Sex drive, 328.
 Shrimps, 75 f.
 Silkworm, 80, 111.
 Simocephalus, 147.
 Size, visual perception of, 217 ff., 242.
 Skin color changes, 144 ff.
 Skin sensitiveness to light, 132 f.
 Skioptic, reactions, 130 f.
 Slug, 193 f., 197 f., 248.
 Smell. *See* Chemical sense.
 Snail, 72, 73, 220, 258, 266, 274 f., 281, 286.
 Space perception, 169, 171, 184, 211; conditions for, 236 ff.; tactical, 235 f.; visual, 213 ff.
 Sparrow, 121, 269, 275.
 Spathidium, 62.
 Spatially determined reactions, 166 ff.
 Spectrum, physiological effectiveness of, 187 ff.
 Speed, of learning as evidence of ideas, 28 ff., 298; of reaction, 211; of maze running, 326.
 Spider, 5 f.; chemical sense, 77; color vision, 158; hearing, 108 f.; learning, 252, 258, 277; light reactions, 193; perception, 239 f.; vision, 216, 231, 235.
 Spirographis, 185.
 Squid, 204.
 Squirrel, 273, 322.
 Squirrel, ground, 281, 337.
 Starfish, 73 f., 138, 162, 215, 248 f., 268.
 Statocyst, 106 f., 171.
 Stentor, 61, 248 f., 252 f.
 Stereoscopic vision, 233.
 Stickleback, 208, 209.
 Structure as evidence of mind, 32 ff.
 Substitutive learning, 336 f. *See* Dropping out of movements.
 Summation of stimuli, 210.
 Support, sense of, 184, 233.
 Surface tension theory, 35 f.
 Surprise, as evidence of ideas, 307 f.
 Suspended reaction, 292 ff., 354; and attention, 343 ff.; and discrimination, 345; and ideas, 310 f.; and space perception, 236 f.
 System-forming learning, 336 f. *See* Movement systems.
 Tadpole, 135, 187.
 Talbot-Plateau Law, 164.
 Taming of animals, 260 f., 266.
 Taste. *See* Chemical sense.
 Tealia, 259.
 Telæsthetic taste, 57.
 Telotaxis, 204.
 Temora, 198.
 Temperature, effect on phototropism, 196 f.; reactions to, 209 f., 250; sensations, 55.
 Temporal maze, 284.
 Temporary modification by experience, 247 ff.
 Termites, 90, 142.
 Tern, 230, 281.
 Thigmotaxis, 60 f.
 Things, perception of, 238 ff., 353.
 Thyone, 74.
 Thyroid, effect of, 328.
 Tiaropsis, 128.
 Time relation of stimuli in learning, 268 f.
 Toad, 263, 265, 275.
 Tonus, 262.
 Topochemical sense, 87, 237.
 Touch, 55, 67; space perception, 235 f.
 Toxopneustes, 131.
 Transfer of training, 320 ff.
 Triton, 100 f.
 Tropism, 15 ff., 133, 185 ff.

- Tropotaxis, 203.
Tubularia, 65, 127.
Turtle, color vision, 160, 163;
 learning, 275; light reactions,
 204; sense of support, 184, 233;
 visual form perception, 218, 220.
Tympanal organs, 111.

Ultra-violet rays, 140 ff., 187, 252.
Unpleasantness, 41, 55, 71, 134,
 249 ff.
Useless movements, dropping off of,
 258 ff., 276 ff.
Useless movement systems, 285 f.

Vanessa, 138, 191, 201, 206.
Variability of behavior as evidence
 of mind, 27 f.
Variety of movements, relation to
 ideas, 312.
Vision, 125 ff.; 211 ff., relation to
 rheotropism, 207 ff.

Visual clues in maze, 282 f.
Visual image, 204; methods of in-
 vestigating, 216 ff.
Visual landmarks in homing, 225 ff.
Visual perception of distance,
 231 ff.
Vitalism, 18, 204, 331.
Volvox, 126 f., 190, 196.
Vorticella, 252.

Wasp, chemical sense, 79, 81, 97;
 homing, 227 ff., 230, 238; ideas,
 294; perception, 239; visual
 form perception, 220.
Water beetle, 110.
Water strider, 79.
Weber's Law, 165.
Wetness, effect on phototropism,
 200 f.
Whiptail scorpion, 134, 193.
Worms. *See* Annelids, Earthworm.

INDEX OF NAMES

- Abbott, 134, 156, 157, 234, 241, 266, 268, 295, 323.
 Aderhold, 172.
 Allabach, 254.
 Allee, 198.
 Allen, 282, 317.
 Alverdes, 132, 193.
 Andreae, 97.
 Andrews, 90, 142.
 Arey, 202, 289.
 Arkin, 191.
 Armbruster, 114.
 Atkins, 307.
 Axenfeld, 206.
 Babak, 144.
 Baldus, 231.
 Baldwin, 314.
 Balss, 76.
 Bancroft, 192.
 Barber, 122.
 Bardeen, 68, 69, 134.
 Bateson, 75, 76, 98, 106, 132.
 Bauer, 159, 216.
 Beer, 18, 107, 234, 235.
 Bell, 75, 76, 212.
 Bentley, 150, 259, 262, 322.
 Bernoulli, 116.
 Bert, 146.
 Bertkau, 77.
 Bethe, 15, 16, 18, 19, 75, 85-92, 94, 95, 108, 114, 225, 226, 239, 263.
 Bierens de Haan, 153, 156, 223, 240, 243, 244.
 Bigelow, 115.
 Bingham, 212, 221, 224, 242.
 Bittner, 192.
 Blauuw, 186.
 Blees, 264.
 Bogardus, 324.
 Bohn, 185, 188, 200, 203, 205, 217, 286.
 Bonnier, 95.
 Bouvier, 229.
 Boys, 108.
 Bozler, 132.
 Breed, 153, 162, 218, 221.
 Brossa, 144.
 Brun, 87, 89, 90, 92.
 Brundin, 199, 203.
 Buddenbrock, 220.
 Bühler, 309 f.
 Burkamp, 155, 163.
 Burt, 302.
 Buttel-Reepen, von, 94-97, 113, 226, 227.
 Buytendijk, 75, 103, 223, 239, 260, 262, 263, 265, 275, 301, 304, 307, 310.
 Carpenter, 201.
 Carr, 278, 281, 283-285, 306, 307, 327.
 Casteel, 218.
 Chidester, 75.
 Claparède, 16, 17, 316.
 Cole, L. J., 218.
 Cole, L. W., 100, 150, 219, 223, 260, 266, 272, 295-298, 325.
 Cole, W. H., 135, 193, 198, 202, 205, 209.
 Copeland, 72, 73, 99.
 Cornetz, 85, 88, 289.
 Cowan. *See* Abbott.
 Cowles, 131, 215.
 Craig, 121.
 Crozier, 134, 192, 193, 197, 202, 289.
 Cyon, 101.
 Dahl, 108, 231.
 Darwin, 7, 14, 70, 92, 235, 340.
 Dashiell, 278, 283, 307, 321, 325.
 Davenport, 162, 173.
 Dawson, 72, 281.
 Day, 262.
 Dean, 135.
 DeCamp, 278.
 Delage, 108.
 Dellinger, 36.

- Demoll, 235, 240.
 Descartes, 12-14.
 De Voss, 156.
 Dice, 196.
 Dodson, 325, 327.
 Doflein, 207.
 Drew, 106.
 Driesch, 18.
 Drzewina, 200, 286.
 Dubois, 130, 131.
 Dufour, 142.
 Dye, 119.

 Ebbinghaus, 308.
 Edinger, 316.
 Eggers, 111.
 Eldering, 218, 275.
 Emery, 112.
 Engelmann, 105, 126, 133.
 Enteman, 227, 294.
 Erdmann, 84, 85.
 Erhard, 161, 163, 165.
 Escherich, 92.
 Essenberg, 79, 196.
 Esterly, 204.
 Ewald, 147, 163, 164.

 Fabre, 82, 227, 229.
 Federighi, 193, 197.
 Ferton, 229.
 Fielde, 90-92, 112, 252, 275.
 Flechsig, 317.
 Fleure, 67, 258.
 Folger, 125.
 Forel, 16-18, 79, 80, 82, 86, 87, 89,
 91, 93, 112, 114, 141, 142, 158,
 205, 220, 237.
 Frandsen, 198, 248.
 Franz, 344, 345.
 Frisch, von, 80, 81, 93, 142, 144,
 145, 154, 155, 157-159, 220.
 Froloff, 117.

 Gamble, 195, 202, 204, 340.
 Ganson, 156.
 Garrey, 193, 208, 209.
 Garth, 275.
 Gee, 186, 286.
 Giersburg, 101.
 Giltay, 93.
 Glaser, 249.
 Goldsmith, 75, 236, 259.
 Graber, 10, 50, 75, 79, 109, 130,
 140.

 Gregg, 298.
 Groom, 196.
 Groos, 313.
 Gurley, 208.

 Hachet-Souplet, 230.
 Hadley, 186, 192.
 Haecker, 259.
 Haenel, 316.
 Haggerty, 299.
 Hahn, 124.
 Hamilton, G. V., 301, 316.
 Hamilton, W. F., 148, 149.
 Hanel, 235.
 Hargitt, 130, 185, 252.
 Harper, 173, 174, 192.
 Hartline, 193.
 Hase, 81.
 Haseman, 286.
 Heck, 263.
 Helms, 283.
 Henke, 324.
 Henning, 104, 160.
 Hensen, 107, 108.
 Herms, 192.
 Herrick, C. J., 98, 259.
 Herrick, F. H., 410.
 Hertel, 219.
 Herter, 55.
 Hess, 130, 131, 138, 139, 142, 148,
 154, 155, 157, 159-163, 187, 191,
 232.
 Hesse, 126, 130, 134, 213, 214, 235,
 252.
 Heymans, 338.
 Hinstedt, 140, 162.
 Hofer, 118.
 Hoffmeister, 340.
 Hoge, 323.
 Holmes, 75-77, 126, 186, 191, 196,
 197, 199, 203, 253, 340.
 Homann, 132.
 Honigmann, 139, 162.
 Hooker, 204.
 Hubbert, 278, 279, 318.
 Hudson, 344.
 Hume, 1.
 Hunter, 121-123, 224, 284, 285,
 292, 293, 295, 299, 300.

 Janet, 112.
 Jellinek, 121.
 Jennings, 35, 36-38, 43, 44, 51, 58-
 60, 67, 125, 168, 173, 189-191,

- 194, 205, 207, 247, 248, 250, 252-255, 339.
 Jensen, 172.
 Johnson, G. R., 192.
 Johnson, H. M., 123, 124, 221, 222, 516.
 Jordan, H., 208.
 Jordan, J., 235.
 Joubert, 132.

 Kafka, 236.
 Kalischer, 123.
 Kanda, 173, 198.
 Katz, 155, 162, 318.
 Keeble, 195, 202, 204, 340.
 Kellogg, 80.
 Kepner, 38, 39, 69.
 Kienitz-Gerloff, 93.
 Kinnaman, 104, 150, 152, 153, 219, 272, 276, 298.
 Kittredge, 156.
 Kline, 11.
 Knoll, 155, 158, 164, 220.
 Köhler, O., 148, 157.
 Kohler, W., 104, 242, 300, 308, 310.
 Kohlrausch, 144.
 Kohts, 153, 223, 244, 301, 328.
 Körner, 115.
 Krall, 315, 316.
 Krause, 133.
 Kreidl, 115.
 Kribs, 71.
 Kroning, 114.
 Kühn, 142, 155, 203.
 Kuo, 278, 324.
 Kuroda, 120, 121.

 Lashley, 121, 151, 152, 162, 278, 279, 319, 320.
 Lee, 115.
 Lehnert, 68.
 Liddell, 326.
 Lindworsky, 309.
 Locke, 3.
 Loeb, 10, 15, 18, 20, 31, 63, 133, 134, 141, 142, 185-189, 192-194, 196-198, 205.
 Löhner, 71, 103.
 Lubbock, 9, 83, 85, 86, 89, 112, 114, 141, 142, 146, 147, 158, 215, 222, 225.
 Lukas, 32.

 Lund, 61.
 Lyon, 172, 173, 197, 206-208.

 McClendon, 38.
 McCook, 77.
 MacCurdy, 131.
 McDougall, 18, 291, 331.
 McDonald, 116.
 McEwen, 202.
 McGinnis, 205.
 McIndoo, 80, 87, 91, 113, 114.
 McPheeters, 298.
 Maday, von, 316.
 Mangold, 121, 235, 236.
 Manning, 118, 120.
 Marage, 115.
 Massart, 172.
 Mast, 38, 44, 126, 137, 139, 144, 145, 164, 187, 189, 190, 193, 194, 196, 197, 250, 301.
 Matthes, 101.
 Mayer, 109.
 Mendelssohn, 210.
 Merejowsky, 146.
 Metalnikow, 61.
 Mills, 10, 11, 184, 272.
 Minkiewicz, 148, 157 f.
 Minnich, 80, 112, 134.
 Mitchell, 275.
 Mitsukuri, 200.
 Mobius, 263.
 Montaigne, 12-14.
 Moody, 62.
 Moore, A., 174.
 Moore, A. R., 141, 174, 195, 205.
 Moore, M. M., 187.
 Morgan, 6, 7, 10, 57, 101, 107, 291, 292, 294.
 Morse, 286.
 Moss, 328.
 Müller, A., 196.
 Müller, G. E., 316, 332.
 Muller, H., 92.

 Nagel, 31, 63, 64, 70, 72, 75, 79, 98, 105, 106, 130, 140, 162, 210, 213, 252, 254, 256.
 Nicholas, 100.
 Norman, 71.

 Obreshkova, 187.
 Oelzelt-Newin, 51.
 Olmsted, 99.
 Oltmanns, 190.

- Orbelli, 223.
 Osten, von, 315.
 Ostwald, 196, 197.

 Parker, 64, 70, 77, 98, 99, 112, 115-118, 133, 191, 195, 197, 199, 201, 204, 206, 217, 220, 254, 255, 286.
 Parshley, 70.
 Patten, 78.
 Pawlow, 52, 156.
 Pearl, 68, 69, 78, 168.
 Pearse, 74, 157, 225.
 Peckham, 5, 6, 77, 97, 108, 158, 227-229, 231, 239, 252, 258.
 Perris, 80, 97.
 Peterson, 277-279.
 Petrunkevitch, 216.
 Pfungst, 315, 316.
 Piéron, 72, 85, 88-90, 254, 256, 258, 281, 286.
 Plateau, 93, 158, 159, 211, 212, 206, 217, 219, 231.
 Plessner, 131.
 Pohl, 155.
 Polimanti, 140.
 Pollock, 63.
 Porter, 221, 231, 269, 270, 275.
 Pouchet, 132, 192, 198.
 Prentiss, 108.
 Preyer, 10, 74, 106, 248, 249.
 Pritchett, 77, 108.
 Pusch, 44.

 Rabaud, 193.
 Rádl, 110, 173, 186, 207, 209.
 Raspail, 101.
 Rawitz, 211, 252.
 Reese, 100.
 Reeves, 154, 159, 165, 212.
 Reichner, 163.
 Reighard, 151.
 Remmers, 260.
 Revesz, 155, 162, 164, 219, 242, 243, 319, 341.
 Rhumbler, 35.
 Richardson, 232.
 Richter, 286.
 Rickey, 329.
 Riekell, 219, 242.
 Riley, 82, 253.
 Risser, 100.
 Rockwell, 281.
 Romanes, 4, 7-9, 28, 29, 67, 73, 102, 103, 106, 131, 232.

 Root, 38.
 Rothmann, 123.
 Roubaud, 209, 340.
 Rouse, 144, 221, 270, 275, 282.
 Rousseau, 11.
 Royce, 33.
 Ryder, 130.

 Sackett, 273.
 Sadovinkova, 275, 302.
 Sams, 279.
 Sanford, 316.
 Santschi, 88, 89, 215.
 Schaefer, 174.
 Schaeffer, 37, 38, 39, 61, 125, 263.
 Scheuring, 235.
 Schiemenz, 142, 152.
 Schmid, 139.
 Schnurmann, 145, 332.
 Schut, 72.
 Schwartz, 171.
 Seffrin, 104.
 Shelford, 99, 247.
 Shepherd, 124.
 Sherrington, 210, 211, 258, 311.
 Simmons, 327, 328.
 Small, 184, 270, 274, 275, 282, 292, 294, 318.
 Smith, A. C., 70.
 Smith, E. M., 156.
 Smith, S., 262.
 Sosnowski, 174.
 Spencer, 338.
 Stein, 198.
 Stevens, 157.
 Stocking, 323.
 Strasburger, 190, 196.
 Strieck, 99.
 Strong, 101, 102.
 Swift, 123.
 Szymanski, 212, 222, 223, 263, 266, 275, 284, 318, 322, 325, 326-328, 331.

 Taliaferro, 38, 69, 191, 193.
 Thompson, 266, 275.
 Thorndike, 7, 10, 15, 223, 260, 269, 271, 272, 275, 276, 277, 290, 292, 294, 295, 331.
 Tiebout, 242.
 Tiedemann, 131.
 Toll, 318.
 Tolman, 278, 279.
 Torrey, 174, 192.

- Tower, 110.
Towle, 199.
Trembley, 134.
Triplett, 115, 263.
Tsai, 308, 328.
Turner, 89, 111, 134, 203, 215, 220,
227, 230, 264, 318.
Uexkull, von, 18, 131, 169, 252,
340.
Ulrich, 319.
Van der Heyde, 92, 261, 286.
Vaschide, 11.
Ven, 268.
Verworn, 10, 105, 106, 172, 184,
188.
Vincent, 278, 282.
Volkelt, 239, 240, 284.
Wada, 121.
Wager, 173.
Wagner, G., 62, 248, 252.
Wagner, W., 95.
Walton, 67, 258, 300.
Warden, 279, 319, 320.
Washburn, 150, 156, 157, 234, 241,
259, 266, 268, 295, 306, 311, 320,
322, 323, 326, 331.
Wasmann, 17, 86-90, 112, 155, 224,
255.
Watson, 18, 20, 101, 102, 145, 151,
152, 230, 276, 281, 285, 317, 325.
Waugh, 152, 232.
Weld, 112.
Wells, 289.
Wenrich, 217.
Wéry, 93, 159.
Westerfield, 117.
Wheeler, 84, 209.
White, A. E., 278.
White, G. M., 153, 260.
Will, 79, 110.
Willem, 211.
Wilson, 134.
Wiltbank, 321.
Wissenburgh, 242.
Woodsdalek, 197, 266, 318.
Wolff, 142.
Wundt, 5, 6.
Yarbrough, 268, 294, 322, 332.
Yerkes, 31-33, 54, 119, 120, 134,
147, 151, 165, 168, 184, 195, 196,
199, 210, 223, 233, 263, 274, 275,
276, 282, 292, 302, 304, 309, 317,
318, 319, 321, 324.
Yoakum, 273, 322.
Yung, 73, 130.
Zeliony, 123, 124.
Zenneck, 116.

